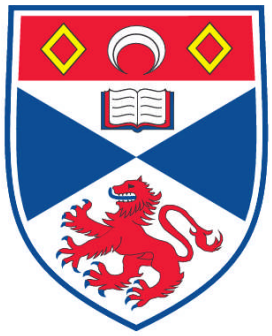
THE VOCAL IMITATION OF BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) SIGNATURE WHISTLES: THEIR USE IN VOCAL MATCHING INTERACTIONS AND THEIR ROLE AS VOCAL LABELS

Stephanie L. King

A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews



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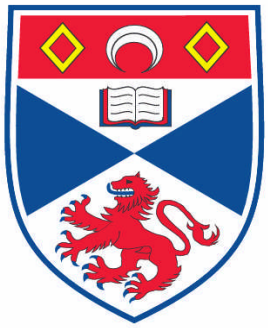

This thesis is submitted in partial fulfilment for the degree of PhD
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Abstract

The bottlenose dolphin uses vocal learning to develop its own unique acoustic signal. This signal encodes the identity of the signaller, and is known as the animal's *signature* whistle. The dolphin's ability for vocal learning means that the signature whistle of one animal may be found in the vocal repertoire of other animals. This copying of signature whistle types may allow conspecifics to label or address one another. This thesis investigated the use of signature whistle copying in both captive and wild animals. Dolphins have been known to rapidly imitate each other's signature whistle in vocal matching exchanges. This matching of sounds has an aggressive connotation in songbirds, yet the function in bottlenose dolphins remains unclear. I have shown, through playback experiments with captive animals, that signature whistle matching in dolphins is not aggressive but appears to be affiliative, and may be used as a tool to initiate contact with the signature whistle owner. In addition, the rapid matching of whistle types in wild dolphins appears to play a specific role in their foraging behaviour, indicating the function of vocal matching may indeed be multi-faceted. This thesis also uses a unique dataset to extensively describe the occurrence of signature whistle copying in wild animals. The imitation of individual signature whistles occurred almost exclusively between close associates during separations. All copies were accurate representations of the original signature whistle, but were clearly recognisable due to fine-scale differences in selected acoustic parameters, and are therefore unlikely to be used deceptively. Finally, I provide evidence that wild bottlenose dolphins respond to hearing a copy of their own signature whistle by calling back. This offers support to the notion that signature whistles function as distinctive labels that are used to address individuals, and perhaps even label them referentially.

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I, Stephanie King hereby certify that this thesis, which is approximately 44,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in November 2008 and as a candidate for the degree of PhD in November 2009; the higher study for which this is a record was carried out in the University of St Andrews between 2008 and 2011.

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Chapter 1

General Introduction

1. Introduction

1.1.1 Individual Identity Signals

Animals that live in highly social groups commonly form long-lasting associations between individual group members and therefore benefit from the development of individual identity signals. Recognition has been best studied in parent-offspring recognition and neighbour-stranger recognition. The recognition of individuals can favour both the signaller and the receiver by allowing parents and offspring to identify one another (Aubin & Jouventin 1998; Aubin et al. 2000) thereby protecting their reproductive success. Neighbour-stranger recognition allows male territory holders to both identify threatening males and to decrease their own harassment by neighbours during territorial interactions. Selection can be placed on receivers who discriminate between individuals more easily, but it can also favour those individuals who broadcast their identity (Tibbetts & Dale 2007). The encoding of identity in acoustic signals may therefore be selected for, allowing animals to discriminate between individuals based on their vocalisations.

Identity can be encoded at the group or at the individual level. Animals may utilise group specific identity calls, that function as a *badge* or *password*, indicating that an animal belongs to a particular social group (Boughman & Moss 2003; Wilkinson & Boughman 1998; Tyack 2008). Animals that exhibit group specific identity calls include the greater spear-nosed bat (*Phyllostomus hastatus*) that use screech calls to co-ordinate group foraging, and these calls differ between groups (Boughman 1997); and black capped chickadees (*Parus atricapillus*) produce flock signatures, with the calls of individuals within each flock converging (Mammen & Nowicki 1981; Nowicki 1989). Killer whales (*Orcinus orca*)

produce learned, group specific call types with a strong matrilineal component (Ford 1991). Sperm whales (*Physeter macrocephalus)* have vocal clans where coda vocalisations pertain to both specific groups and higher-order clans (Rendell & Whitehead 2003). Recent evidence, however, purported to underlying individual signatures in one specific coda type in this species (Antunes et al., 2011).

Animals can also encode identity in individually specific signals by developing individually distinctive call types. Falls (1982) and Beecher (1982) both highlight that signals for individual recognition should favour high inter-individual variability and low intra-individual variability. Individual recognition may therefore be heightened when the variation of identity signals between individuals is maximised and the variation within an individual is minimal. There is, however, large variation in the mechanisms that encode this individual identity, varying from individually specific or 'unique' vocal signatures to individual acoustic differences in the same call type. These individual acoustic differences are individually distinctive signals or '*by product distinctiveness'* that have evolved under natural selection due to differences in vocal tract morphology and body size (Boughman & Moss 2003). These differences may be selected for over evolutionary time to help increase distinctiveness, as in signature calls in the greater horseshoe bat (*Rhinolophus ferrumequinum*). Here the frequency of a pup's calls is partly determined by its mother (Jones & Ransome 1993) and similarity may be increased through vocal learning. Other animals also use voice cues to discriminate between individuals; such as with squirrel monkey (*Saimiri sciureus*) isolation peeps (Symmes et al., 1979).

Truly unique individual signatures or '*designed individual signatures'* are developed through vocal learning (Boughman & Moss 2003). These *designed individual signatures,* or specific vocal signatures, appear to be rare in the animal kingdom, with the largest body of evidence coming from bottlenose dolphins (*Tursiops truncatus*). Dolphins produce unique individual signatures that are developed within the first year of life through vocal learning (Fripp et al., 2005; Miksis et al., 2002; Tyack & Sayigh 1997). Individual identity in these

calls is encoded in their unique frequency modulation pattern independent of voice features (Janik et al., 2006). For the bottlenose dolphin, the compression of the vocal tract at depth means that *by product distinctive* calls would be unreliable. Voice cues such as timbre change with depth are therefore unreliable indicators of identity, but the frequency contour of the whistle appears to be unaffected by depth (Madsen et al. 2011).

1.1.2 Vocal Learning

A select number of animals use vocal learning to acquire new sounds. Vocal production learning is a skill that is common in birds but less so in mammals. (Janik & Slater, 1997; Snowdon, 1990). Vocal production learning allows animals to incorporate new sounds into their acoustic repertoire (Janik & Slater 2000). Animals can copy novel sounds in their environment and develop their own individually distinctive repertoire of calls. In some species vocal learning influences male song, which is a reproductive advertisement display with an acoustic structure that is selected through intra- and inter-sexual selection. This is true for birds (Catchpole & Slater, 2008), seals (Janik & Slater, 1997), and baleen whales (Janik 2009b). Other species use vocal production learning to develop individual or group distinctive identity signals; delphinids (Janik 2009a), bats (Boughman 1998; Knornschild et al., 2010), and elephants (Poole et al., 2005). This vocal plasticity opens an additional avenue to using complex copying skills.

Vocal imitation allows individuals to generate a large repertoire of sounds and is a second key innovation in the evolution of spoken language (Fitch 2000). Signal copying can function in addressing or labelling selected conspecifics (Tyack 1993). This may be through the initial copying of another conspecifics individually distinctive call or via vocal matching of individual or group specific calls.

The rapid matching of acoustic signals has been discussed as a mechanism that allows individuals to direct a signal towards an intended receiver (Krebs et al., 1981; McGregor et al., 1992). The great tit (*Parus major*) responds to the playback of songs from their own repertoire by singing the same song type back (Krebs et al., 1981). The authors found that song matching was associated with an approach by the matching individual. Thus the matching of song types can be used to direct a graded signal of aggressive intention between two territorial males. Vocal matching may well convey reliable information about distance between the signaller and receiver, known as '*the distance signalling hypothesis'* (Falls et al., 1982; Krebs et al., 1981; Todt & Naguib 2000; Morton 1982). It may facilitate information exchange between conspecifics by revealing distance (Falls 1985; Falls et al., 1982; Krebs et al., 1981). The distance signalling hypothesis would only make sense with dolphins if they were able to use acoustic cues, such as degradation, to measure distance to a sound source; see chapter 2 for an in-depth discussion on vocal matching and the '*distance signalling hypothesis'*.

1.1.3 Bottlenose Dolphin Signature Whistles

The bottlenose dolphin produces a variety of communicative sounds. These include broadband echolocation clicks, broadband burst-pulsed sounds, and narrow-band frequency modulated whistles (Popper 1980). Bottlenose dolphins live in a fission-fusion society where animals associate in small groups that change in composition on a daily or hourly basis (Connor et al., 2000). More stable individual relationships are also formed, such as between mother-calf pairs and long-lasting male alliances (Smolker & Pepper 1999; Watwood et al., 2004). This contrasts with another delphinid species, the killer whale, which forms stable matrilineal groups and uses group specific call types (Ford 1991). Instead, the bottlenose dolphin forms a more fluid social system with animals forming a variety of different social relationships.

The fission-fusion social system of bottlenose dolphins has likely led to selective pressure for individual recognition (Sayigh et al., 1999). Bottlenose dolphins have high encounter rates with one another and therefore are likely to develop an extensive network of vocal recognition. Although they have excellent vision, this is restricted in an underwater environment. Identity is therefore transmitted through the acoustic channel which has led to the selection of individually specific signature whistles that function as a contact call (Caldwell & Caldwell 1965; Caldwell et al., 1990; Sayigh et al., 2007; Fripp et al., 2005; Miksis et al., 2002; Tyack & Sayigh 1997). Natural selection may have favoured individuals developing unique vocal signatures that facilitate accurate recognition (Tibbetts & Dale 2007) and even vocal labelling (Tyack 1993).

In captive or temporarily restrained wild animals, the signature whistle is the most common or only whistle type produced, making them easy to identify (Caldwell et al., 1990; Sayigh et al., 2007). Recent work has shown that in free-ranging wild animals, signature whistles can be identified by their stereotypy and temporal sequencing, with most occurring within 1 – 10 seconds of one another (Janik et al., in press). Signature whistle use in wild animals comprises 38% to 70% of their whistle vocalisations (Buckstaff 2004; Cook et al., 2004; Watwood et al., 2005). The frequency of their use depends on social context (Janik & Slater 1998; Cook et al., 2004). Signature whistles function in both individual recognition and in maintaining group cohesion and thus can be used to reunite or locate individuals (Janik & Slater 1998; Sayigh et al., 1999).

Janik *et al.* (2006) showed that signature whistles contain identity information that is encoded in their unique frequency modulation pattern that is developed by each individual early in life. There appears to be no influence of relatedness on whistle similarity between bottlenose dolphin mothers and their female calves (Sayigh et al., 1995) but some male calves may develop signature whistles that are similar to their mothers (Sayigh et al., 1995). In other studies signature whistles of related individuals do not seem to be more similar to each other than those of nonrelated individuals (Janik et al., 2006). In fact dolphins may model their

signature whistles on community members they rarely associate with (Fripp et al., 2005). However, long-lasting male partnerships can result in an increased similarity between signature whistle types over time (Smolker & Pepper 1999; Watwood et al., 2004).

Although the signature whistle is a stable component of an animal's repertoire (Sayigh et al., 1990), their capability for vocal learning means they can incorporate new sounds into their repertoire throughout their life (Richards et al., 1984). This means that the signature whistle of one animal can be copied by other animals (Janik & Slater, 1998; Tyack, 1986, 1991; Tyack & Sayigh, 1997). The copying of signature whistles has been studied in two adult captive bottlenose dolphins (Tyack 1986). Tyack's study demonstrated vocal imitation with the use of a telemetry device attached to the animal. The telemetry device lit up when the animal vocalised. The study showed that the animals imitated each other's signature whistles at rates near 20%. The accuracy in their imitative abilities varied in precision between the two animals. There are, however, doubts as to how representative a 20% vocal imitation rate is in wild animals. The high copying rates in this study may have been attributed to motivational cues, particularly with visual stimuli such as the vocalight telemetry device.

With the exception of this study, copying events seem to be rare (Janik, 2000; Janik & Slater, 1998; Watwood et al., 2004), yet significantly more common than expected by chance (Janik 2000). The rare copying of signature whistles prevents confusion as the signature whistle itself remains a reliable indicator of identity of the owner.

Janik et al.'s (2006) study highlighted the independence of the identity information in signature whistles from general voice features. Individuals responded preferentially to the synthetic signature whistle of a related rather than a familiar individual. This preference was shown to be independent of kin discrimination, or whistle similarity. This led to the possibility that signature whistles are used as referential signals, by either addressing individuals or referring to them. Tyack (1993) proposed the *signature labelling hypothesis*;

where bottlenose dolphins may copy signature whistles to initiate contact with the owner. This would be equivalent to calling an animal by its 'name'.

In our own communication system, vocal labelling or naming is one of the defining features of human language thought to set us apart from other animals. This capacity for referential signalling allows us to communicate about objects and events that are external to us (Macedonia & Evans 1993). There is evidence that some species use referential signals in the form of alarm calls for different predator classes (Seyfarth et al., 1980). Yet, unlike naming in humans, there is little evidence that animals can use referential signals for different social companions. In recent years one study (Wanker et al., 2005) showed that spectacled parrotlets (*Forpus conspicillatus*) use different vocal labels for different family members. In order to be considered as referential a signal should meet both production and perception criteria (Evans 1997; Macedonia & Evans 1993). The signal should be both acoustically discrete with a high degree of stimulus specificity, and the receiver response to the signal should be elicited even in the absence of contextual information (Evans 1997; Macedonia & Evans 1993). Wanker et al. (2005) argue that the contact call in spectacled parrotlets meet both these criteria.

If signature whistles are to be used as social referents, then potential cues must be present to distinguish between a signature whistle copy and the signature whistle emitted by the owner. If copies are only produced in exchange between two animals, where one names the other, then this may not be important. For receivers outside of the dyadic interaction, however, cues would allow them to discern between a copy and an original. It would prevent the distinction between the two becoming blurred and signature whistles becoming unreliable in reporting identity.

An alternative hypothesis may be that such whistle copying is used as a deceptive form of signalling, although this remains unlikely. Deceptive mimicry has previously been a hypothesis for the adaptive significance of song copying in songbirds (Payne 1983). This is

not the case in song sparrows (*Melospiza melodia*) at least; song sharing is associated with reduced aggression between neighbours, but the mechanism is not deceptive mimicry (Wilson & Vehrencamp 2001). Song sparrows discriminate between a true neighbour and a mimic seemingly by memorising subtle differences in a given neighbour's song type that facilitates individual recognition (Wilson & Vehrencamp 2001). These subtle differences may be aligned with voice characteristics or variation in fine details of the song type.

There is evidence to suggest that subtle differences are encoded in signature whistle copies. Two captive bottlenose dolphins were shown to produce each other's signature whistle (Tyack 1986; Tyack 1991). The adult female tended to include more amplitude modulation in her version of her male pool mate's signature whistle. Further work is required on whether subtle differences occur in signature whistle copies across other individuals.

Bottlenose dolphins are known to be able to discriminate between whistle contours that appear to vary ever so slightly (Harley 2008). Therefore, parameter differences may function as cues that enable individuals to discriminate between the signature whistle owner and the mimic. This discriminability would facilitate their use as referential signals; used to address or to refer to individuals either singly or in vocal matching events. It may also allow a third party to know whether a signal is a copy and even who the copier is. Although bottlenose dolphins may also occasionally copy the signature whistles of absent conspecifics (Watwood et al., 2005), in all reported cases of signature whistle copying and where the identities of the animals are known, it has been the owner of the signature whistle that called first (Janik 2005; Janik & Slater 1998). This opens the possibility that instead of addressing an animal first, an individual could also address a social companion by copying its signature whistle in a vocal matching event. Vocal matching can be used as a tool to initiate contact with the signature whistle owner if the receiver rapidly reproduces a signature whistle copy after hearing the original signature whistle. Songbirds are well known for their ability to use song type matching to address males during territorial disputes (Bremond 1968; Krebs et al. 1981; Falls et al. 1982). So far, bottlenose dolphins are the only mammal, with the exception

of humans, to undertake vocal matching with learned, individually specific signal types (Janik 2000). This notably rare skill for complex vocal imitation makes them an interesting subject of study for understanding the evolution of spoken language (Fitch 2000).

1.2 Thesis Overview

That signature whistles may be used as descriptive labels either to address individuals or to refer to them is an intriguing hypothesis. It is not, however, known how referential these descriptive labels may be. I explore the role of the vocal imitation of signature whistles in the bottlenose dolphin communication system. I also investigate the role of vocal matching and compare its use across taxa.

I begin the thesis by examining research on vocal matching and I propose a set of criteria to help define the term in the wider literature (Chapter 2). I then address the topic experimentally and describe sound playback experiments with captive bottlenose dolphins. In songbirds, vocal matching appears to be a signal of aggressive intent (Burt et al., 2001; Searcy & Beecher 2009; Beecher et al., 2000) yet in the bottlenose dolphin the copying or matching of signature whistles is hypothesised to function as an effective signal of addressing individuals (Tyack 1993). I test this hypothesis in Chapter 3 by vocally matching animals with a synthetic version of their signature whistle after they produce it. I use signature whistles of different animals as controls. Although interactive playback has been extensively used in studies on songbirds (McGregor et al., 1992; Nielsen & Vehrencamp 1995) this is the first controlled interactive playback experiment on vocal matching in a nonhuman mammal.

Vocal matching has also been discussed as a way for animals to facilitate localisation by assessing caller distance (Falls et al., 1982; Krebs et al., 1981) and it may play a role in cooperative foraging. In Chapter 4 I investigate the use of vocal matching in wild bottlenose dolphins and describe its correlation with foraging behaviour.

In Chapter 5 I investigate the vocal imitation of individual signature whistles in temporarily-restrained wild animals. In this study vocalisations are ascribed to individual animals via suction cup hydrophones. Data spanning 25 years were analysed for occurrences of signature whistle copying. These vocal imitations were compared to the original signature whistle (as produced by the owner) and the copier's own signature whistle. I investigate whether there are systematic differences between the copy and the original that may act as acoustic cues to receivers. I also address which members of the community copy each copied dolphin. This is the first study to provide a cross-sectional analysis on the imitation of individually specific calls.

The function of signature whistle copying is worthy of exploration. I addressed this experimentally by conducting playback experiments with wild bottlenose dolphins (Chapter 6). In this study I recorded the signature whistles of wild animals *in situ*, created a synthetic version, and played the synthetic signature whistle back to my focal group. This allowed me to produce a vocal 'copy' of an animal's signature whistle, essentially 'addressing' the animal, and observe the response in a natural setting.

In summary, the aim of this thesis is to explore the use and imitation of these learned individually specific identity signals. We know dolphins have the ability to use novel, learned signals to label objects referentially (Richards et al. 1984). We also know they use learning and innovation to develop their own unique labels in the wild (Janik et al., 2006; Sayigh et al., 2007). Therefore signature whistles may be used as referential signals in the natural communicative system of wild bottlenose dolphins (Janik et al., 2006; Tyack 1993).

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Chapter 2

Vocal Matching: Forms and Functions

2.1 Vocal Matching

2.1.1 History of Vocal Matching

During the last few decades of animal communication research one of the most important vocal interactive behaviours that has been studied is vocal matching (Beecher et al., 2000; Bremond, 1968; Burt et al., 2001; Falls, 1985; Falls et al., 1982; Janik, 2000; Krebs et al., 1981; Lemon, 1968; McGregor et al., 1992; Miller et al., 2004; Schulz et al., 2008; Stoddard et al., 1992; Sugiura, 1998; Todt, 1981; Todt & Hultsch, 1996; Tyack, 1986). Vocal matching can be described as a receiver responding to a signal by changing some features of its own vocal behaviour in order to imitate the preceding signal.

Previous definitions in the literature have varied between studies and include; (1) *"Song matching occurs when a bird responds to playback or a rival by singing phrases from its repertoire which resemble the stimulus song"* (Krebs et al., 1981); (2) *"…if a bird hears a song of a type that it has in its own repertoire, it can match by responding in kind or it can fail to match by singing a different song"* (Falls, 1985); (3) "*…the bird replies to a stimulus song by singing the song type in his repertoire that most resembles it. This is called type matching"* (Searcy & Beecher, 2009); (4) '*Matching interactions were defined as an occurrence in which two whistles of the same type produced by separate individuals occurred within 3 seconds of each other"* (Janik, 2000); (5) "*Call matching ..[is].. the number and complexity of calls that are produced by a male are approximately matched by its neighbour*" (Gerhardt et al., 2000); (6) *"[Matching is] ..temporarily associated vocal exchanges"* (Schulz et al., 2008).

It is believed that matching interactions may function as a mechanism for individuals to direct a signal towards an intended receiver (Bremond, 1968; Janik, 2000; Krebs et al., 1981; Miller et al., 2004; Schulz et al., 2008; Sugiura, 1998), for receivers to confirm reception of a signal (Schulz et al., 2008), or for conspecifics to exchange information on their location or some other variable (Falls et al., 1982; Krebs et al., 1981).

Vocal matching was reported as early as 1958, followed by a succession of experimental work on a variety of bird species (Bertram, 1970; Bremond, 1968; Hinde, 1958; Lemon, 1968), and through anecdotal observations (Gompertz, 1961). The phenomenon of vocal matching, although evident in some bird species, was found to be absent in others (Falls & Krebs, 1975). Ideas were generated on the function of vocal matching, with a variety of hypotheses being put forward. Armstrong (1973) related song type-matching to antiphonal duetting in a pair of birds, where it 'names the opponent' in a song duel. Alternatively it was suggested that song type-matching regulated the intensity of song interactions within a duet (Lemon, 1968). Bertram (1970) mentioned that vocal matching may even be equivalent to 'flinging an insult back at a rival' in a form of territory competition. There was, as yet, no evidence to support any of these hypotheses.

In 1981 Krebs and colleagues' experimental approach showed that great tits (*Parus major*) responded to the playback of 'own songs' (from their own repertoire) by singing the same song type. Individuals also approached the speaker closely upon matching the playback, and as such matching may be seen as a reliable signal of a close approach. The authors proposed the '*threat hypothesis'*; they predicted that type-matching functioned as a '*graded signal'* directed between two individuals in a territorial dispute, and therefore there is a correlation between the probability of matching and the response strength resulting in an increased likelihood of attack. This increased likelihood was not, however, found to be the case in other studies with the great tit (Falls et al., 1982) or with the western meadowlark (*Sturna neglecta*) (Falls, 1985). Krebs and colleagues (1981) also predicted that type-matching events between neighbours should occur at higher frequency in the beginning of the

breeding season when territories are first established, and this should dissipate later on in the breeding season. That territorial disputes occur at higher frequency during the breeding season is a sign of the major shift in the reproductive and motivational state of the animal. This prediction has been corroborated in later studies with the song sparrow (*Melospiza melodia*) and the great tit and the use of interactive playback (Beecher & Campbell, 2005; McGregor et al., 1992; Nielsen & Vehrencamp, 1995).

Interactive playback may give a greater insight into signal value (McGregor et al., 1992). The invention of interactive playback in the field of animal communication has allowed the rapid interaction between the experimenter and the study subject (McGregor et al., 1992). Krebs et al.'s initial predictions have thus been examined in far greater detail. It has previously been shown that the songs of established territory neighbours are less threatening to the subject than songs of strangers which are type-matched at much higher rates (Falls 1985; Stoddard et al., 1992). Instead of type-matching a neighbour a bird may instead choose a different song from a repertoire shared with its neighbour; known as repertoire matching (Beecher et al., 1996). This requires knowledge of the neighbours' repertoire which can be perceived as affiliative. Burt et al. (2001) used interactive playback to show that birds are less likely to escalate into a contest when repertoire matched in comparison to when they are type-matched.

Repertoire matching is not matching in the strictest sense and is not discussed further in this chapter; instead I concentrate on type matching where two animals produce the same call type. This contrast, however, between type and repertoire matching may be seen as a signalling strategy which leads to graded levels of contest escalation with repertoire matching de-escalating a contest. It is worthwhile considering the idea of a discrete signal that transmits information with a graded level of motivation or elicits a graded receiver response. The evolutionary benefits of a graded signal system to both the signaller and receiver are to indicate different levels of intention to escalate a contest, and thus graded signals may be used to establish territorial boundaries (Krebs et al., 1981).

2.1.2 Signalling Strategies

Interesting inferences on the function of vocal matching can be drawn from dyadic interactions in songbirds. Todt and Naguib (2000) discuss both the time and pattern specific responses of songbird vocal exchanges; the premise being a receiver may respond to a signaller by either adjusting the timing of its song output, or by using a song pattern that is 'linked in some way' to the pattern used by the signaller (Todt & Naguib, 2000).

Animal communication is governed by temporal rules (Kureta, 2000; Masataka & Biben, 1987; Nakahara & Miyazaki, 2011; Sugiura, 1993). These rules allow animals to assess vocal exchanges and determine whether an individual is directing a call towards an intended receiver or is calling independently. Individuals may synchronise or alternate their call production as a way of mediating social interactions. Insects will synchronise their chirps in multi-male chorusing (Greenfield & Shaw, 1983; Otte, 1977), as will frogs (Wells 1977; Klump & Gerhardt 1992). The alternation of calls, where individuals alternate their call production, is seen in duetting gibbons and oscines. Vocal matching involves the co-ordination of calls between individuals. More than two individuals can participate in a vocal match, where they co-ordinate the timing of their calls. Call overlap can occur during vocal matching events; however, if more than 2 individuals are repeatedly overlapping one signal type then the interaction may be similar to chorusing. Chorusing can be described as synchronous calling, where a large number of individuals 'sing' or call in unison.

Bremond (1968) and Todt (1981) both hypothesised that vocal matching may serve to address a particular individual, with Todt (1981) suggesting that the timing of the match may encode a more specific message. Todt considered both rapid matching and delayed matching (where an animal waits until after the signaller has called), with the former hypothesised as a 'vocal threat' or being agonistic in nature as it was associated with high arousal, and the latter as a more affiliative exchange or 'vocal greeting' as it seemed to occur when birds were less aroused (Todt, 1981; Todt & Hultsch, 1996). Overlapping of the same signal type between

two individuals occurs in highly escalated vocal contests in some bird species (McGregor et al., 1992; Vehrencamp 2001). Overlapping may be seen as an extension of rapid matching and therefore be agonistic in nature, although this remains an area of contention (Naguib & Mennill, 2010; Searcy & Beecher, 2009, 2010). In contrast, if a respondent delays a vocal match until after the signaller has called then vocal interference is avoided and more subtle information, encoded in the calls, can be exchanged between the individuals (Todt & Naguib, 2000). Although many studies have extensively discussed vocal matching as agonistic in function, an increased rate of matching during intense disputes may in fact be used to direct the response towards the matched individual and may not be agonistic in itself (Todt & Naguib, 2000). As such the signal value of matching is linked to the temporal scale of the response. Thus Todt and Naguib (2000) eloquently surmise that … "*[vocal] matching is not a simple response but rather leads to a highly complex form of signalling*".

2.1.3 Familiarity versus Similarity

Further studies on vocal matching have revealed that a birds' decision to match is also based on how similar a song is to the same song type in its own repertoire (Great tit in Falls et al., 1982; western meadowlark in Falls et al., 1988; song sparrow in Stoddard et al., 1992). These studies demonstrated that birds were more likely to match a playback when the stimulus was very similar to their own rendition of the same song. As a consequence neighbours were matched more often than strangers in some species (Falls et al., 1982), but not in others (Falls, 1985). Song learning and dispersal patterns in some species lead to shared levels of similarity of song types with neighbours which can lead to higher rates for matching (Beecher, Campbell & Nordby, 2000). However, when this effect of similarity was controlled for, there was a tendency for a bird to match strangers more than neighbours (Falls et al., 1982). Stoddard et al.'s (1992) work with the song sparrow also showed the highest matching rate by individuals was to the playback of their own song. In addition, stranger song provided a much stronger stimulus than neighbour song when equated for similarity (Stoddard et al.,

1992). These studies highlight the importance of familiarity versus similarity in signal types. Birds show a preference to match songs that are highly similar to their own renditions, sometimes leading them to match neighbouring males. When this similarity is controlled for, however, the bird will type match strangers more than neighbours. It is likely that males recognise their neighbour's song repertoire, and (once similarity is controlled for) song-type matching may reflect uncertainty as to the identity of the singer, if the signer is a stranger then it is more likely that a bird will match the song-type (Stoddard et al., 1992).

2.1.4 Distance Signalling Hypothesis

Vocal matching may well convey reliable information about distance of both the signaller and receiver, known as '*the distance signalling hypothesis'* (Falls et al., 1982; Krebs et al., 1981; Todt & Naguib 2000; Morton 1982). It was suggested that vocal matching in birds occurs in order for individuals to exchange information on their distance from one another (Falls et al., 1982; Krebs et al., 1981; Morton, 1982; Todt & Naguib, 2000).

In 1981 Richards proposed the hypothesis that birds could use amplitude or degradation cues to estimate the distance of singing conspecifics. It was already known that birds responded more strongly to song played in the middle of their territory than song played at the edge or outside of their territory (Dhondt, 1966; Falls & Brooks, 1975). Richards (1981) therefore believed that the responding bird could recognise that those songs were more distant. This hypothesis was extended by Morton (1982) who suggested birds would judge degradation of a song by comparing it to a *standard* (most similar song) from its own repertoire. This became known as the '*ranging hypothesis*'. The theory of ranging is that a receiver can determine the distance of a known signaller by becoming familiar with the repertoires of known individuals as well as the degradation effects of sound transmission in the local environment (Hopp & Morton, 1998). The fine details inherent in the structure of any acoustic signal are liable to degrade rapidly as distance between signaller and receiver increases (Falls et al., 1982). Degradation is thought of as a more reliable indicator than

amplitude because amplitude does not change in a predictable manner with distance and it is under the control of the singer (McGregor et al. 1983). Numerous studies have shown that songbirds can estimate the distance between themselves and a counterpart by ranging; species that use ranging include Carolina wrens (*Thryothorus ludovicianus*) (Richards, 1981); great tits (McGregor & Krebs, 1984; Mcgregor et al., 1983) and western meadowlarks (McGregor & Falls, 1984). The studies provided evidence that the birds responded less strongly to degraded song playbacks than undegraded songs.

Krebs (1981), Morton (1982) and Falls et al. (1982) went on to suggest that when territorial neighbours are song type matching they can exchange information on their distance by ranging, known as the '*distance signalling hypothesis'*. Although matching is not required in order to range a signal, it would allow both the signaller and the receiver to exchange accurate information about their distance from one another. It provides an undegraded template against which the extent of degradation can be assessed by and the range to the caller estimated. It therefore benefits both singers, particularly between established neighbours who can use it to confirm territory boundaries, and are not thought to represent a threat to one another (McGregor et al. 1983).

2.2 Vocal Matching in Delphinids

Although dolphins are not territorial and do not sing, we may draw on the vocal matching studies in birds and discuss the similarities it may have with signature whistle matching in the bottlenose dolphin (*Tursiops truncatus*). Dolphins use their acoustic signals in the context of social interactions and group cohesion. A comparison of the contexts of vocal copying in delphinids and song birds would help us to evaluate whether the occurrence of matching with learned signals is a universal indicator of aggression in different taxa or whether it can have other functions.

Wild bottlenose dolphins have been shown to overlap stereotyped whistles during vocal matching interactions (Janik, 2000). We know bottlenose dolphins use stereotyped signature whistles that promote individual recognition (Janik et al., 2006; Sayigh et al., 1999). Group members therefore may know the place and identity of individuals as a result of these vocal exchanges (Nakahara & Miyazaki, 2011). It is believed signature whistle matching may function as a mechanism for initiating or maintaining contact with specific individuals concurrent with the '*signature labelling hypothesis*' (Tyack, 1993). Killer whales (*Orcinus orca*) also type match group specific calls when out of visual range of one another (Miller et al., 2004). In line with the '*distance signalling hypothesis*', delphinids may vocally match to exchange information on their distance from one another which may promote certain behaviours, such as co-operative foraging. In mobile species both group cohesion and the co-operative aspects of foraging behaviour may be maintained by sound source localization (Miller, 2002), or assisted by ranging.

Bottlenose dolphins may also vary the timing between vocal matches in order to indicate their level of intention, motivational state or urgency to reunite. As with some birds, rapid matching events or overlapping may imply a level of aggression or urgency, whereas delayed vocal matching may denote a rather different function. It is conceivable to think that vocal matching has an interchangeable function that is dependent on both the motivation and intention of the respondent, and that this information is encoded in the temporal sequencing of the vocal match.

The bottlenose dolphin is not known to be territorial and therefore is not under the same social pressures as most bird species. As such, dolphins may not strongly respond upon hearing an unfamiliar signature whistle. The fission-fusion society of the bottlenose dolphin coupled with the effective transmission of sound underwater result in an environment rich in communicative signals. An animal may waste time and energy responding to those calls it is not familiar with. Anecdotal data have shown that wild bottlenose dolphins react strongly when their own signature whistle is played back to them by calling back or moving towards

the speaker (V.M. Janik, pers. comm.). These animals also respond strongly to signature whistles of familiar, related individuals in comparison to familiar, unrelated individuals (Sayigh et al., 1999; Janik et al., 2006). It may well be that bottlenose dolphins would show the greatest response strength to copies of their own whistles and the lowest strength of response to strangers, whose signature whistles they are unfamiliar with.

In comparison to songbirds, vocal matching in delphinids remains poorly understood. It may be agonistic in function, or more likely to occur in aggressive contexts, as shown in some songbirds where individuals use learned song types in matching interactions during territorial disputes with unknown callers (Beecher et al., 2000; Burt et al., 2001). Some species undertake more subtle forms of vocal matching. In the Japanese macaque (*Macaca fuscata*) the subtle matching of acoustic parameters during vocal exchanges is more likely to occur between affiliated individuals (Sugiura, 1998). In the squirrel monkey (*Saimiri sciureus)* animals produce similar calls to promote partner preferences (Biben et al., 1986). There is evidence that animals will produce acoustically similar calls as a means of social affiliation. Male chimpanzees (*Pan troglodytes*) will modify their calls to make them acoustically similar when participating in chorus bouts (Mitani & Brandt, 1994). This similarity is higher between closely associated individuals, although there is no evidence that this last example constitutes a form of vocal matching. Instead it may reflect context calling with shared calls where animals vocally accommodate one another.

Signature whistle matching may therefore have an affiliative role and allow animals to address one another via their individually distinctive calls; it may also enable dolphins to exchange information about their respective locations or distance from one another, analogous to the '*distance signalling hypothesis*' in birds (Falls et al., 1982; Krebs et al., 1981). For bottlenose dolphins it is the changes in both the acoustic parameters of the copied whistle, the temporal patterning of the matching, and the distance between the interacting animals, that may indicate the motivation behind the use of signature whistles in matching interactions. The formation of hypotheses on the function of vocal matching, and the incorporation of a strict

experimental protocol, can certainly begin to shed light on how signature whistle matching may function in the complex vocal repertoire of the bottlenose dolphin.

2.3 Defining Vocal Matching in a Broader Framework

To date, there is no clear distinction in the literature as to what defines a vocal matching event and therefore the term is often freely used to describe a range of vocal interactions that occur between individuals. This is largely attributed to the methods undertaken. A vocal match should occur more often than expected by chance in order for it to reflect an interaction: i.e. does not occur by chance alone. An individual must also reproduce a signal of the same type in order to perform a vocal match. In any given species, groups of individuals may share call types and therefore vocal matching may occur completely at random. In many species, individuals will produce the same call type as a result of an external stimulus, known as context calling. One must therefore consider whether a vocal interaction between two individuals is a true interaction, in which a receiver's response is specific to the signaller, or whether the interaction is an artefact of signallers calling in response to the same stimulus (Todt & Naguib, 2000). Caution should be applied when using the term vocal matching to describe vocal interactions.

A select number of studies have reliably demonstrated vocal matching. The most extensive of these are in the bird literature (Beecher et al., 2000; Burt et al., 2001; Falls, 1985; Krebs et al., 1981; McGregor et al., 1992). Vocal matching has also been reliably shown in the bottlenose dolphin (Janik, 2000), a species that uses an individually specific call, and the killer whale (Miller et al., 2004) and the sperm whale (*Physeter macrocephalus*) (Schulz et al., 2008) who both use group specific calls. These interactions were shown to occur at a higher proportion than expected by chance. By using a short time window, in which two calls of the same type had to occur to be considered a match, the authors were able to distinguish true vocal matching from the matching of same call types as an artefact of context calling. Another species, the Japanese macaque matches the acoustic properties of conspecific coo

calls (Sugiura, 1998). The coo call is a contact call and has a high degree of variability in the fundamental frequency. Sugiura (1998) found that a fast or frequent vocal matching response by an individual resulted in a decrease in call structure similarity. This species may not, therefore, be able to undertake rapid vocal imitation. They do, however, have the ability to match the acoustic features of the vocal response to some degree, and because two or more animals may produce coo calls at any one time, the acoustic matching allows the preceding callers to *'…discriminate between a true response and an independent call'* (Sugiura, 1998). An animal's ability to vocal match is likely to be more advanced in those species that have the ability to accurately imitate novel sounds. Those animals that are capable of vocal copying, such as delphinids and oscines, are likely to be far more advanced in their use of vocal matching.

There have also been studies in the wider literature that are unconvincing in their reporting of vocal matching. This includes the discussion that alarm calling in some nonhuman primate species constitutes vocal matching (Balsby & Bradbury, 2010). Diana monkeys (*Cercopithecus diana*) are one such species. They live in female groups with one adult male. The adult males use long distance calls, which are produced spontaneously as well as to a variety of stimuli (Zuberbuhler et al., 1997). In some instances a male will produce a long distance call after hearing a long distance call produced by a neighbouring male. Although this may seem to be an occurrence of vocal matching, any given male will also produce this call after a tree falls, in reaction to predator presence and also without any apparent stimulus. The application of a statistical technique, such as rotation randomisation tests (Miller et al., 2004), may reveal that the production of this call after a neighbouring male produces the same call is not vocal matching but merely down to chance. In addition, the females respond to a male's long distance call with their own acoustically very different alarm calls. The fact that their responses are acoustically different is strong evidence against vocal matching under the definition that I propose. To date there is no evidence offering support to the occurrence of true vocal matching during alarm calling in guenons, as proposed by Balsby

& Bradbury (2010). Future studies should aim to implement tools to look at the temporal sequencing of these species' call production. Another study is Gerhardt et al.'s (2000) on the quacking frog (*Crinia georgiana*). Male anurans have been reported to alternate calls with neighbouring conspecifics, believed to be a form of mate competition. The study found that males sometimes matched the combined number of pulsed notes in calls produced by their two nearest neighbours. The male frogs, however, in this study generally did not precisely match the number of notes in a conspecific stimulus call. The authors acknowledged that in order to ascertain true modification of calling behaviour playback experiments should be conducted with stimulus calls with different dominant frequencies (Gerhardt et al., 2000). A male frog would need to either modify its pulsed calls to match the dominant frequency of the stimulus call or match the number of notes above chance levels to meet the first and third point of my definition (to follow).

Some studies have also claimed that vocal matching occurs in a species of psittacine (Balsby & Bradbury, 2010). The study is, however, unconvincing, as there is no evidence of the animals matching specific acoustic properties of one another's chee call. The authors found convergent, divergent and variable patterns of call type similarity in response to chee call playbacks. If true vocal matching occurred between individuals then consistent convergent patterns should be evident when context is controlled for. A statistical analysis may well highlight that these convergent patterns are down to chance. Vehrencamp et al., (2003) conducted playback experiments with orange-fronted conures (*Aratinga canicularis*); playing back conspecific chee calls to flocks of conures. The authors claim that the response strength to the playback strongly correlated with maximum similarity between respondent and stimulus calls. They chose, however, the respondent chee call from the flock that was most similar to the stimulus. This is not convincing evidence of true vocal matching and also may be due to chance. In addition, similarity of respondent calls to the stimulus seemed to increase during the first minute or two after the playback and then decrease. If true vocal matching was occurring then we would expect a respondent to produce the call with the highest level of

similarity immediately following the playback. An alternative explanation is that the animals tune their response to become more and more similar to the playback, although one could argue this is more similar to vocal accommodation than vocal matching. If an animal wanted to direct a response towards a signaller it would need to produce the match immediately, allowing the preceding caller to discriminate between it being a true response and not just an independent call, as highlighted by Sugiura (1998). One method which could be used to validate, or otherwise, the presence of true vocal matching is a bout analysis, as exemplified by Sugiura (1998).

In order to understand the different abilities of a species to vocal match, and the processes they undertake to achieve this, a definition is required on what parameters define a vocal match. Although previous studies on vocal matching in songbirds have been clear on the definition used, the diffusion of this term into the wider literature has led to the current definition becoming somewhat unclear. The term is now used to describe a whole range of vocal interactions. I propose that a vocal interaction should meet all of the following criteria in order for it to be considered a true vocal matching event:

i. The signal emitted by animal B is a repetition of the signal pattern emitted by animal A; there may be slight variation in pitch, amplitude and duration but the acoustic and temporal features are matched as accurately as possible; animal B copies the signal pattern of signal A, or reproduces the pattern that most closely resembles signal A from its repertoire. The extent of accuracy possible may depend on which call parameters are salient to the animal i.e. frequency, temporal etc. for example, songbirds should reproduce the song from their repertoire that is most similar to the initial song or anurans should produce the call from their repertoire with the tempo that is most similar to the initial call.

ii. The signal is repeated within a short time window following the emittance of the signal by animal A. It is the first signal emitted by animal B upon hearing signal A.

iii. The reproduction of this signal should have value, where the individuals are interacting vocally for a specific purpose, and should therefore occur at a higher proportion than expected if it were down to chance when context is controlled for.

In addition, tools can be implemented that may assist in confirming a vocal interaction as a true matching event:

i) Statistical Techniques

Statistical tests may be used to look at the timing of call sequences, as exemplified in other studies (Sugiura 1998; Miller et al., 2004; Janik 2000; Schulz et al., 2008), such as bout analyses and randomization tests. Vocal matching can be examined by statistically describing an animal's calling behaviour. Different behavioural contexts can be accounted for by using a bout analysis (Sibly et al., 1990; Slater & Lester, 1982). This involves examining the timing of a particular call type. Call type production may differ between bouts depending on what behaviours are occurring. If animals are calling in bouts then these bouts can be identified and each bout can be treated separately. Studies have used this method to determine whether calls were produced in response to a stimulus or at random (Sugiura, 1998). The method has also been used to control for the specific contexts of calling exchanges. Miller et al., (2004) used the method and criterion in Sibly et al., (1990) and Slater & Lester (1982) to calculate whether a group of free-swimming killer whales were calling in bouts.

Randomisation tests can then be used to test for matched counter-calling within each bout, controlling for the context specificity of bouts. Randomisation tests have been used in a number of studies on vocal matching in order to preserve call timing and to determine whether matched counter-calls were produced above chance levels (Miller et al., 2004; Schulz et al., 2008; Janik 2000). Vocal matching may occur by chance if some acoustic, visual or olfactory stimuli causes animals to all produce the same call type at once, such as alarm calling in nonhuman primates (Seyfarth et al.,1980). In these cases, it may appear that animals are vocal matching because they all produce the same call type within a short time interval. Studies addressed this by incorporating a short time criterion in which two calls have to occur in order to be considered a true vocal match, and they must occur within this time window at higher levels than expected by chance. Animals that are calling at random, due to an external stimulus, may cluster their calls soon after a stimulus and then call production may decline in rate. Under these circumstances calls may be clustered within a calling bout but under different circumstances they may be distributed randomly throughout a bout. True vocal matching and context calling may therefore be difficult to tease apart. The use of a randomisation test addresses this by comparing observed call distribution with the distribution expected if animals were calling at random within a vocal bout. For example, within a bout, animals may all produce the same call within the same time period as a response to an external stimulus. This may then appear to be vocal matching. However, when the randomisation test shuffles the timing of these calls within the bout and the number of calls occurring within a short time window are recalculated a similar high correlation of calls over time is expected, if the length of the bout is relatively short. The randomisation test would then show that the observed matching did not occur above chance levels.

Another way to address this problem is to take recordings of focal individuals and observe calling behaviour at the individual level. Researchers could then focus on dyadic exchanges between individuals and, with the incorporation of a short time window, identify vocal matching interactions between pairs of animals. The occurrence of vocal matching between

dyadic animals may be easier to identify. If many animals produce the same call type in response to an external stimulus, this may be not be vocal matching in the strictest sense, but is more analogous to chorusing. Therefore by incorporating a short time window, focusing on individual vocal behaviour and analysing calls in bouts, researchers can distinguish between vocal matching as a signal and the matching of same type calls as an artefact of context calling.

ii) Playback Experiments

Sound playbacks have been used in numerous studies with birds to see if they are capable of vocal matching and to elicit its function. Such experiments can be used to identify responses of an animal to being vocally matched and can be used to define the time window for defining vocal matching. Playback experiments allow finer scale questions to be addressed, such as the role of similarity versus familiarity of the call stimulus in prompting matching responses from individuals.

iii) Long Term Studies

What is equally important to using statistical techniques and conducting playback experiments is the knowledge of the call repertoire for individuals of the study species. Does the species in question produce individually specific calls, group specific calls, or perhaps species specific call types? To understand whether vocal exchanges constitute vocal matching interactions, one must have an understanding of the vocal repertoire at an individual level, and utilise spectrographic analyses in order to ascertain whether the sounds produced in matching interactions are the most similar sounds from the animals' repertoire to the sound it is matching.

In the next few chapters I draw on this definition and look at the use of vocal matching in bottlenose dolphins. We know dolphin signature whistles are individually specific, learned signals (Caldwell & Caldwell, 1965; Caldwell et al., 1990; Fripp et al., 2005; Miksis et al., 2002; Sayigh et al., 2007; Tyack & Sayigh, 1997). As such, the copying of another dolphin's signature whistle is an obvious example of the animal changing some of features of its own vocal behaviour in order to imitate another animal's individually specific call. I subsequently use both playback experiments (Chapter 3) and randomisation tests (Chapters 4 & 5) to establish whether true vocal matching takes place and to investigate and explore its function.

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Chapter 3

Vocal Matching with Signature Whistles in the Bottlenose Dolphin (*Tursiops truncatus*)

3.1 Introduction

Vocal matching is a powerful mode of interaction utilised by a select number of animals, namely songbirds (Searcy & Beecher 2009), odontocetes (Janik 2000; Miller et al., 2004; Schulz et al., 2008), and primates (Sugiura 1998). By rapidly matching an acoustic signal a receiver can direct a response towards the preceding signaller. (Janik 2000; Krebs et al., 1981; McGregor et al., 1992; Miller et al., 2004; Sugiura 1998). Vocal matching is therefore an effective way of addressing individuals (Janik 2000; Tyack 2000; Todt 1981).

Bremond (1968) and Todt (1981) both hypothesised that vocal matching may serve to address a particular individual, with Todt (1981) suggesting that the timing of the match may encode a more specific message. Temporal associations are known to govern vocal exchanges in animals (Nakahara & Miyazaki 2011; Kureta 2000; Sugiura 1993; Masataka & Biben 1987). The kind of vocal exchange that I am considering is regulated by the timing of the calls, where an animal that is addressed with a signal replies within a short time interval. These rules allow animals to determine whether an individual is directing a call towards an intended receiver or is calling independently. The matching of call types also requires that the signaller pay attention to what call another animal has just produced. The same call type must be given by different individuals and must occur within a short time window in order to be considered a vocal match. Temporal rules therefore also govern vocal matching interactions. Previous studies that have

explored vocal matching in animals have incorporated an arbitrary criterion for this time window: 10 seconds for song sparrows (*Melospiza melodia;* Beecher et al., 2000); 5 seconds for killer whales (*Orcinus orca;* Miller et al., 2004); 3 seconds for bottlenose dolphins (*Tursiops truncatus;* Janik 2000); and 2 seconds for sperm whales (*Physeter macrocephalus;* Schulz et al., 2008). It is not yet known, however, how short this time window should be in any species as far as its salience to the animals themselves is concerned. One way to address this would be to conduct sound playback experiments and simulate vocal matches at different time intervals after the signaller calls to determine how short this time window should be.

Vocal matching has been extensively described in songbirds and odontocetes. These animals share vocal learning, a skill that is rare in animals. Vocal learning has been observed in song birds, hummingbirds, parrots, bats, pinnipeds and cetaceans (Janik & Slater 1997), elephants (Poole et al. 2005) and primates (Egnor & Hauser 2004; Fitch 2000). Vocal matching of song types in songbirds appears to signal aggressive intent, with it more likely to occur in aggressive contexts (Beecher et al., 2000; Burt et al., 2001; Searcy & Beecher 2009), allowing males to address each other in agonistic displays during territorial defence. In other taxa, animals use matching to maintain acoustic contact, indicating that not all forms of vocal matching are agonistic in function. Japanese macaques (*Macaca fuscata*) match calls with group members (Sugiura 1998) and killer whales (Miller et al., 2004) and bottlenose dolphins (Janik 2000; Chapter 5) match group and individually specific calls respectively.

Bottlenose dolphins are adept vocal learners and are highly proficient at vocal mimicry. To date dolphins are the only nonhuman mammal that has been found to undertake vocal matching with learned, individually-specific signal types (Janik 2000). Their aptitude for complex vocal imitation therefore makes them an interesting subject of study to shed light on the evolution of spoken language (Fitch 2000). Bottlenose dolphins use vocal learning and innovation to

develop arbitrary signature whistles. These whistles function both in individual recognition and in maintaining group cohesion (Janik & Slater 1998; Sayigh et al., 1999). Signature whistles are the most common whistle type produced by a dolphin when isolated from group members, making them easy to identify (Caldwell et al., 1990). Signature whistle use in wild, free-ranging animals ranges from 38% to 70% of their whistle vocalisations depending on social context (Buckstaff 2004; Cook et al., 2004; Watwood et al., 2005). An animal's individual identity is encoded in the unique frequency modulation pattern of the signature whistle (Janik et al. 2006), and is developed by each individual early in life (Fripp et al., 2005; Miksis et al. 2002; Tyack & Sayigh 1997). These contact calls of bottlenose dolphin have more inter-individual variability than those of other animals. Thus their signature whistles allow them to transmit individual identity more reliably (Tyack 2000).

Dolphins are known to copy each other's signature whistles and occasionally produce these in matching interactions (Janik & Slater 1998; Tyack 1986; Chapter 5). Tyack raised the interesting possibility that bottlenose dolphins copy signature whistles to initiate contact with the owner. This differs from matching as it requires an animal to produce a copy of another animal's signature whistle first, as if calling it by name. Yet in all reported cases where both signature whistle matching has been observed, and the identities of the callers were known, it was the 'owner' of the signature whistle that called first (Janik & Slater 1998; Janik 2005). Therefore animals may use vocal matching as a tool to initiate contact with the signature whistle owner, by replying to the signature quickly after the owner produces it. The receiver can direct a response towards the signaler by matching the preceding call and thereby opening up a two-way communication channel between the two individuals. If signature whistle matching is used as a signal to address specific individuals, then it should have a higher probability than expected by chance of an animal responding to the match.

To investigate the hypothesis that signature whistle matching functions as an effective signal for addressing individuals, I conducted a series of playback experiments at three different captive dolphin facilities. When an animal produced its signature whistle it was either subjected i) to a playback of its own whistle (a vocal match) or ii) to a playback of a signature whistle from a different animal (control). I hypothesized that signature whistle matching would elicit responsive calling in the target animal. In addition, to investigate how soon after the original sound the match should be produced if it was to elicit a response I incorporated a time delay to the playback experiments. In an underwater environment that is rich in communicative signals I predicted a rapid match would elicit a stronger response and a delayed match would elicit a weaker response. Animals are known to adjust fine-scale parameters of their call as a result of changes in their motivational state (Janik et al., 1994) or to encode additional information (Biben et al., 1986). Signature whistles produced before and after a vocal match were therefore compared in order to determine whether dolphins modified their whistle as a result of being vocally matched.

By uncovering the functional significance of vocal matching with learned, individually distinctive signals in the bottlenose dolphin we may uncover their use as distinctive labels that are used to address individuals.

3.2 Methods

3.2.1 Subjects

The experimental playbacks took place at three dolphinaria; The Seas Aquarium, Orlando, USA during May – June 2009; Zoo Duisburg, Germany during March-April 2010; and Dolphin Quest, Bermuda during February – March 2011.

The Seas Aquarium

The subjects were four captive, adult male bottlenose dolphins (*Tursiops truncatus*); Ranier was 28 years old and was caught in the Gulf of Mexico when he was 3 years of age. The other males were Khyber (18 years), Calvin (15 years) and Malabar (8 years), and were all captive-born. All four animals were unrelated, with the exception of Khyber and Calvin who had the same father. All four animals had been together for the previous 3.5 years; Ranier and Calvin had been together for 6 years. The dolphins were housed in an indoor facility and usually kept in pairs, with one pair in the main tank (20,318 m^3 cylindrical pool with a diameter of 28m and a depth of 8.2m) and the second pair in two interconnected back pools that could be separated from the main tank by two watertight gates. The animals had constant acoustic contact but only had visual contact through one of the watertight gates during playback sessions. The playbacks occurred in the two back pools, which were each approximately 100m^3 (56 m^2 in area with a 2m depth).

Vocalizations were recorded with two HTI-96 MIN hydrophones (frequency response: 0.002 to 30 kHz ±1 dB) and two CRT hydrophones (C54XRS; frequency response: 0.016 to 44 kHz, C54XR ±3 dB; frequency response: 0.016 to 50 kHz ±3 dB) onto a Toshiba Satellite Pro laptop using a 4 channel Avisoft 416 UltrasoundGate recording device (sampled at 50 kHz, 8 bit;

frequency response: 0.02 – 370 kHz ± 3 dB). The caller was identified using passive acoustic localisation (Janik & Slater 1998).

Video recordings were taken using two digital video cameras mounted above the back pools and from a third analogue VN37CPH underwater camera attached to a Sony Handcam DCR-HC96E and recorded onto mini DV tapes. The Sony Handcam also had an acoustic input from one of the HTI-96 MIN hydrophones.

Zoo Duisburg

The subjects were 6 captive animals: 1 adult male, 3 adult females and 2 calves. The adult male, Ivor, was 31 years old, and had been caught in the Gulf of Mexico (age at capture unknown). Pepina was 28 years old; she had also been caught in the Gulf of Mexico (age at capture unknown). The other two adult females, Delphi (17 years old) and Daisy (14 years old) were both born at the facility. The 2 calves were both 3 years old at the time of study. They were Donna (calf of Pepina) and Dolly (calf of Delphi). Unfortunately the playbacks were not successful at this facility. The animals had no prior experience with sound playback experiments and were not habituated to having equipment placed into the pool. No playback treatments were conducted and the study was terminated after 3 weeks.

Dolphin Quest Bermuda

The subjects were 7 animals: 4 adult females and 3 calves. Cirrus was 37 years old and had been caught in the Gulf of Mexico (age at capture unknown), she was the only female without a calf at the time of study. Both Bailey (22 years old) and Caliban (18 years old) were captive born and all 3 of these females had been housed together at Dolphin Quest for the last 15 years. The fourth

adult female was Ely (8 years old) and she was born at the facility to the female Bailey. The 3 calves were all 11 months old at the time of study. The 2 female calves were Cavello (calf of Bailey) and Marley (calf of Ely); the male calf was Cooper (calf of Caliban).

The animals were kept in outdoor tidal pools with a floating dock, and therefore had both constant acoustic and visual contact. The animals could move freely between the pools and were kept in different group compositions that changed on a daily basis. The playback pool was 120 m^2 in area with depth dependent on tide. The vocalisations of the animals were recorded with four HTI-96 MIN hydrophones (frequency response: 0.002 to 30 kHz ±1 dB) onto a Dell Laptop using a 4 channel Avisoft 416 UltrasoundGate recording device (sampled at 100 kHz, 8 bit; frequency response: 0.02 – 370 kHz ± 3 dB). Whistles were localised to an individual using the TOADY localisation program (Quick et al., 2008).

Video recordings were taken from an analogue VN37CPH underwater camera attached to a Sony Handcam DCR-HC96E and recorded onto mini DV tapes. The Sony Handcam also had an acoustic input from one of the HTI-96 MIN hydrophones. I was unable to film the response of the target animals for every playback trial and therefore only a subset of the playbacks conducted at Dolphin Quest Bermuda were analyzed for behavioral responses. TOADY localisation was used to determine whether the initial whistle and the response to the playback came from the same location.

All of the animals both at the Seas and at Dolphin Quest had previous experience with experimental playbacks of natural dolphin whistle sounds.

3.2.2 Experimental Playback

Sounds were played back through a Lubell LL916 underwater speaker (Lubell Labs Inc, Columbus, Ohio; frequency response: 600 Hz-21 kHz ±8dB) connected to a Magnat classic 1000 XL car amplifier (frequency response: 0.005 – 100 kHz ± 3 dB). Stimuli were played back from a Toshiba Satellite Pro laptop using the Avisoft 416 Ultrasoundgate with Avisoft RECORDER v3.4 (Avisoft Bioacoustics, Raimund Specht, Berlin; frequency response: 0.02 – 370 kHz ± 3 dB). The source level of the playbacks conducted at both facilities was 121 ± 5 dB re. 1 µPa (rms) at 1m. The source level was measured with a calibrated Reson TC 4013 hydrophone, a Reson VP 1000 voltage preamp and a Tucker-Davis Technologies RX6 multifunction processor. Sound acquisition was on a Dell laptop with MatLab. In both facilities the speaker was kept in the same location for all sound playback experiments.

3.2.3 Playback Stimuli

The study involved waiting for the target animal to produce its signature whistle and then playing back that very same whistle type in a synthetic version thereby matching the target animal. The signature whistles of the target animals were identified by recording the most common whistle produced by the animal when isolated from group members (Caldwell et al., 1990). A number of signature whistle versions were chosen and synthesised for each target animal and used for the matching treatment. The use of synthesised whistles avoided some of the motivational cues that may be associated with a specific signature whistle version.

The playback controls used in this study consisted of the signature whistles of 8 different wild animals from Sarasota Bay, Florida. These whistles were recorded during capture-release events conducted annually for the health assessment of these animals (Wells et al., 2004).

Signature whistle controls of 2 captive adult bottlenose dolphins from Zoo Duisburg, Germany were also used as controls for the animals at Dolphin Quest, Bermuda. In addition, for both facilities the signature whistle of a non-target animal from the same captive group was incorporated as a control to try and address any potential problem with familiarity versus unfamiliarity. All of the whistles used as stimuli in the playbacks were synthesised using SIGNAL v 4.0 (Engineering Design, Berkeley, CA), (see method in Janik et al., 2006). Average sound pressure levels were equalised for each stimulus.

3.2.4 Playback Protocol

The playback trials involved waiting until the target animal emitted its signature whistle, at which point I would then either simulate a vocal match by playing back a synthetic version of the animal's own signature whistle (the same whistle pattern) or I would play back a control; the signature whistle of another animal (different whistle pattern). As stated previously, the control whistle could either be the signature whistle from an unfamiliar or a familiar animal. A temporal parameter was also incorporated in the design by introducing different time delays between the target animal producing its signature whistle and the start of the playback. The time delays ranged from overlapping the target animal to producing the playback up to 15 seconds after the target animal produced its signature whistle, resulting in only a small proportion of the whistles being overlapped. If another animal vocalized before I began the playback, the trial was not included for further analysis. Recordings were viewed in real-time so that I was able to see immediately when the target animal vocalized, and playbacks were then conducted simultaneously with the recording using Avisoft RECORDER. The playback treatments were randomised in their playback sequence. Playback treatments were conducted when the animals were involved in no activities with the animal trainers.

3.2.5 Eliciting Whistles

A playback design was implemented to try and elicit signature whistle calling in the target animal to help boost sample size of the playbacks. The playback design relied on the target animal producing its signature whistle. Captive animals often remain quiet for extended periods of time. It is known that signature whistle use in captive animals primarily occurs when animals are separated from one another (Janik & Slater 1998). Therefore, based on the finding by Janik & Slater (1998) that, when one animal is isolated from the group and emits its signature whistle, other animals also primarily use their signature whistles a playback set-up was designed that elicited signature whistling in the target animal. If animals were quiet for more than 15 minutes, the signature whistle of one of the non-target animals from the same facility was played back up to 7 times over a 30 second period. This invariably initiated signature whistle calling in the target animal. Upon the target animal producing its signature whistle the playback of the non-target animal was ceased and one of the playback treatments was played. The benefit of this playback design is that it gives control of the motivational state of the animal prior to the treatment playbacks as context is controlled for.

3.2.6 Data Analysis

The acoustic recordings of the playbacks were analysed by inspecting the spectrograms (FFT length 1024, overlap 100%, Hanning window) in Adobe Audition v2.0 (Adobe Systems). All statistical procedures were conducted in R (R project for statistical computing; GNU project). The animals' vocal responses to the different playback treatments were recorded. A GLM with a binomial family was used to analyse the variation in initial vocal response to the playback treatments. The type of vocal response (signature whistle or none (including variant whistles))

was treated as the binary response variable. The following predictor variables were modelled: playback treatment (categorical), animal identity (categorical) and the time delay of the match in seconds (continuous). Model fit was checked by R^2 for binary data (Naglekerke 1991). An interaction term between animal identity and treatment was incorporated to explore the relationship between individual responses to playback treatments.

For the matched playback treatment the target animal's signature whistle was compared before and after the vocal match (if produced) to see whether the animals adjusted temporal or frequency parameters of their signature whistle as a result of the match. The signature whistle contours (frequency modulation pattern) were extracted using a supervised contour extraction program (Deecke & Janik 2006). The whistle contours had a time resolution of 5ms and the following parameters were measured: start frequency, end frequency, minimum frequency, maximum frequency and duration. The number of loops was also measured; a loop was defined as a repeated modulation pattern within a signature whistle that could be separated by periods of stereotyped silence of up to 250ms (Esch et al., 2009). A pairwise comparison was performed for each of the parameter measurements. An F test to compare variances was conducted followed by a paired t test.

The behavioural responses to the matching and control playback trials were compared in order to ascertain whether animals adjusted their behaviour in response to being vocally matched. The following continuous variables were measured: time (seconds) spent in the playback pool, time (seconds) spent in a different pool, time (seconds) spent within 3m (one body length) of the playback speaker, time (seconds) spent at more than 3m (one body length) of the playback speaker (in the playback pool). Swim speed was also measured. This was based on a 4-point index which differed between the two facilities. At the Seas: 1 (still), 2 (slow circling: 12-15 seconds spent each side of the pool), 3 (circling: 6 seconds each side of the pool), and 4 (fast

swimming and splashes/tail slaps). At Dolphin Quest: 1 (still), 2 (slow circling: 25-30 seconds each side of pool), 3 (circling: 8 -12 seconds each side of pool), 4 (fast swimming, 2-6 seconds each side of pool, splashes/tail slaps). The criteria differ due to the differing pool sizes at the two facilities and were calculated to ensure the speeds measured were equalised between facilities. All measurements were taken during a 1-minute period after playback. Due to the strong correlation between variables a principal component analysis was used to derive a single composite behavioural response score (McGregor et al., 1992). A total of 7 observations were removed to achieve multivariate normality. The first two component factors accounted for 91% of the variance and were used to calculate the scores. A two-tailed Wilcoxon rank sum test was used to test whether animals responded differently to the two playback treatments.

The presence or absence of immediate behavioural reactions (jaw clapping, tail slapping, and repeated burst pulsed sounds) was also noted in order to ascertain whether vocal matching induces aggressive states (Overstrom 1983) as can occur with type matching in songbirds.

3.3 Results

I conducted a total of 110 playback experiments to the 7 different animals from the two different captive groups. Of these 61 were own signature whistle (vocal match) playbacks and 49 were different signature whistle (control) playbacks.

Table 3.1. The study animals with the number of playback experiments they were subjected to for the two different signature whistle (SW) treatments, own (vocal match) and different (control), and the number of times they replied with their signature whistle in brackets.

			Playback Treatments	
	Sex	**Age**	**Own SW (match)**	**Different SW (control)**
Ranier (The Seas)	M	28 years	18 (17)	17 (4)
Khyber (The Seas)	M	18 years	4 (4)	2 (0)
Cirrus (DQ Bermuda)	F	37 years	16 (16)	12 (7)
Bailey (DQ Bermuda)	F	22 years	10 (6)	11 (1)
Caliban (DQ Bermuda)	F	18 years	3 (0)	0
Cooper (DQ Bermuda)	M	11 months	7 (2)	5 (0)
Cavello (DQ Bermuda)	F	11 months	3 (2)	2 (0)

The Seas

The 4 adult males in this facility were predominantly quiet and so the playback design, used to elicit whistles, was employed. Only 2 out of the 4 males responded to the playbacks (where a non-target animal's signature whistle was played) and produced their own signature whistles. A total of 99 whistle-eliciting playbacks were conducted over 28 days to these adult males (Khyber and Ranier). These playbacks elicited 34 vocal responses from Ranier and 6 vocal responses from Khyber and a treatment playback followed each (Figure 3.1).

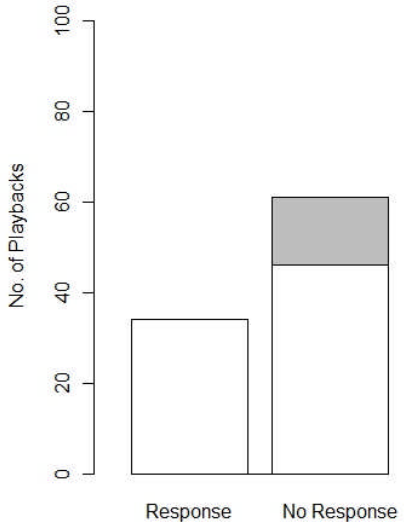

Figure 3.1: The number of times the target animals at The Seas either responded to the initial playback stimulus (signature whistle of a pool mate) by producing their signature whistle, or did not respond to said stimulus. The shaded area represents the last 4 days of the experimental trials where 15 playback trials occurred and the animals never responded.

The fact that these animals responded strongly to the signature whistle of a known conspecific by producing their own signature whistle highlights the importance of signature whistle use in maintaining group contact or cohesion. One additional playback was done with Ranier when he called spontaneously (see Table 3.1).

On average 3.4 (range: 2-6) playback trials were conducted on a given day with a trial lasting on average 7.8 minutes (range: 3-28). The average latency between the stimulus whistle and the target animal's response was 0.56 seconds (range from 0–2.9; Figure 3.2a). The mean number of stimulus whistles played back to the target animals in order to elicit a signature whistle response was 2 (range from 1 to 7; Figure 3.2b).

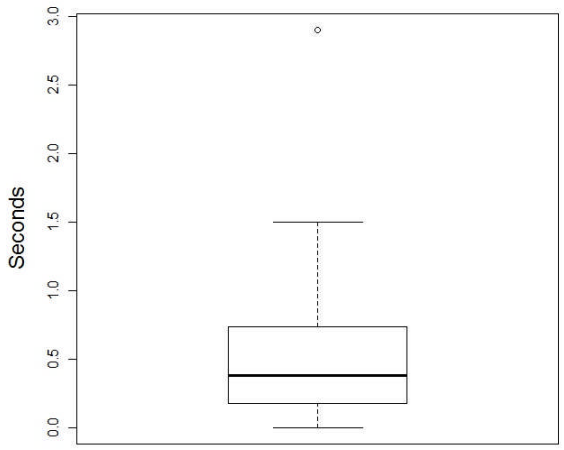

Figure 3.2a: Boxplot of the latency between the non-target stimulus whistle and the target animal's vocal response.

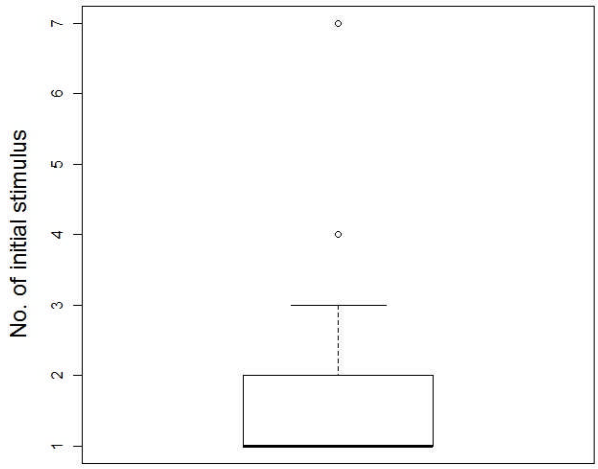

Figure 3.2b: Boxplot of the number of non-target signature whistle stimuli played in order to initiate signature whistle calling in the target animal.

Dolphin Quest

The 7 bottlenose dolphins at this facility were more vocal than those in The Seas and playbacks were largely conducted when the animals vocalised spontaneously. A total of 113 playbacks were conducted over 16 days. Only 11 of the playbacks involved a playback component that used a non-target animal as a stimulus. Playbacks were only included in the analysis when confirmation was available that it was the target animal who had vocalized. All playbacks where the wrong signature whistle stimulus had been played (excluding controls) or the identity of the caller was in doubt were removed from further analysis. This gave a total of 69 successful playbacks from 5 different target animals (see Table 3.1). On average 9.1 (range: 2-22) playback trials were conducted on a single day. On average a playback session would last 1 hr 25 mins (range: 42 mins – 3 hr 22 mins).

3.3.1 Do animals respond to being vocally matched?

The difference in vocal response to the two different playback treatments was significant (GLM, $p<0.0001$; Table 3.2) with evidence of good model fit ($R^2 = 0.7$). The relationship between the animals' responses to the different treatments is shown graphically in Figure 3.3.

Table 3.2. GLM results; estimates and p values comparing the initial vocal response of the animals to treatment (own signature whistle or different signature whistle) playbacks.

	Estimate	SE	Z value	Pr(>|z|)
Intercept	- 0.92	0.49	- 1.87	0.06
Treatment (Own)	2.84	0.59	4.79	< 0.0001
Time	- 0.20	0.09	- 2.25	0.02

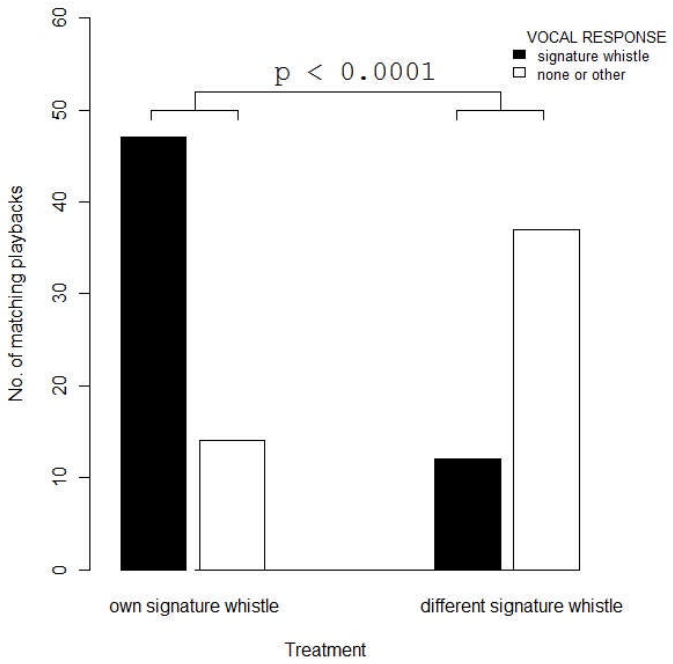

Figure 3. 3. The vocal response of the 7 captive bottlenose dolphins to being vocally matched by either their own signature whistle or to a different signature whistle (control). The vocal response is either that the target animal produces its signature whistle (black) or that it produces was no response or another vocalisation (white).

The results reveal that the vocal response of an animal being vocally matched by its own signature whistle (the whistle it had just produced) is to reciprocate the match, and that is significantly different to the response of the animal when a different signature whistle (control) is played (examples given in Figure 3.4 a-c). There is therefore a significantly higher probability that an animal that is vocally matched will respond by matching back. Animals never responded to the control treatments by matching the control stimuli. They were mostly silent, and occasionally produced a variant whistle. The interaction term in the model between animal identity and response to playback treatments revealed no significant differences between individuals and was subsequently removed from the model under stepwise selection.

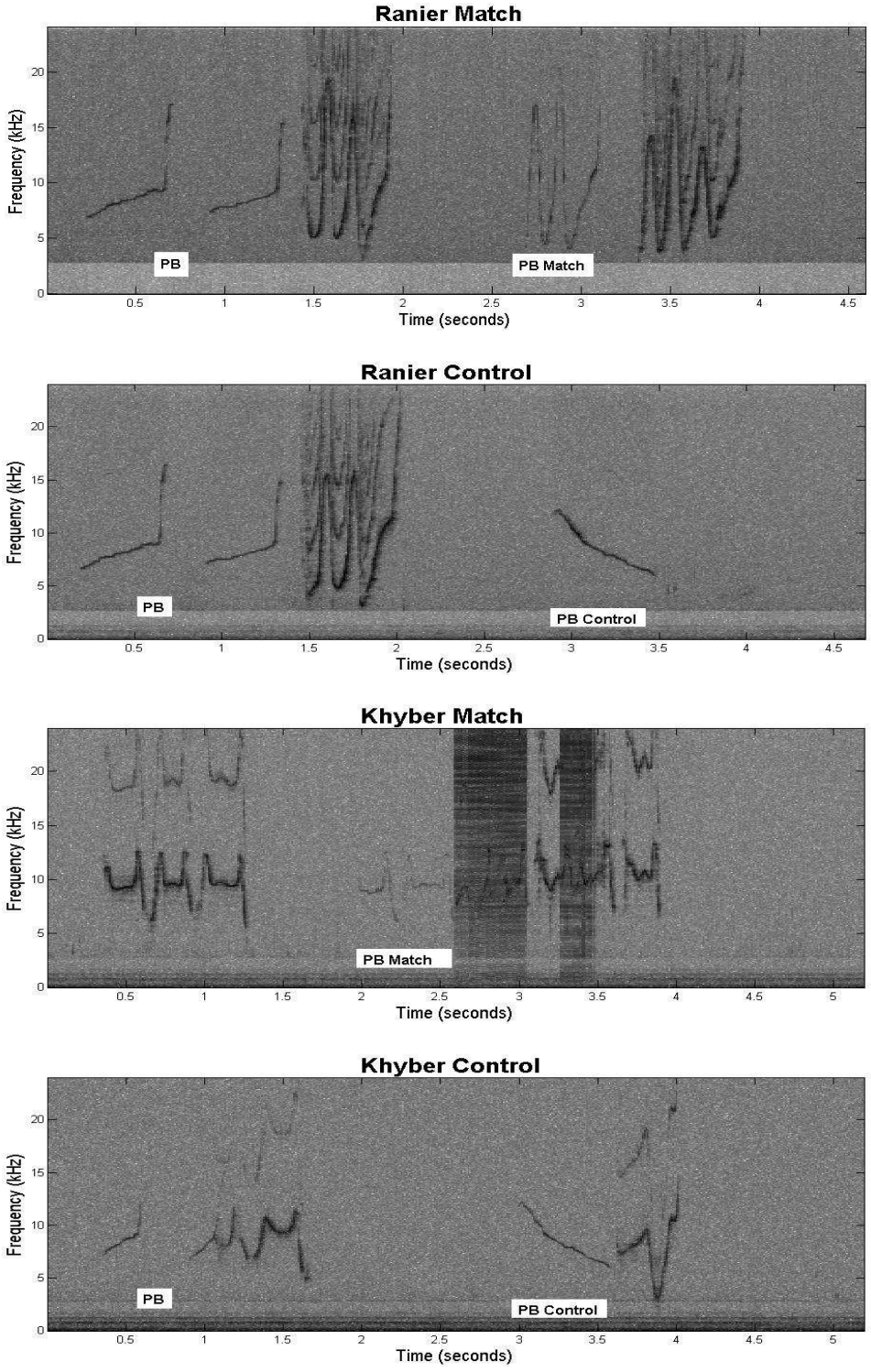

Figure 3.4a. Spectrograms showing an example of a matching playback and then a control playback for each of the adult males respectively (Ranier and Khyber): sampling rate is 48000 Hz, FFT length 1024, Hanning window function. The playback stimuli are highlighted with the label "PB".

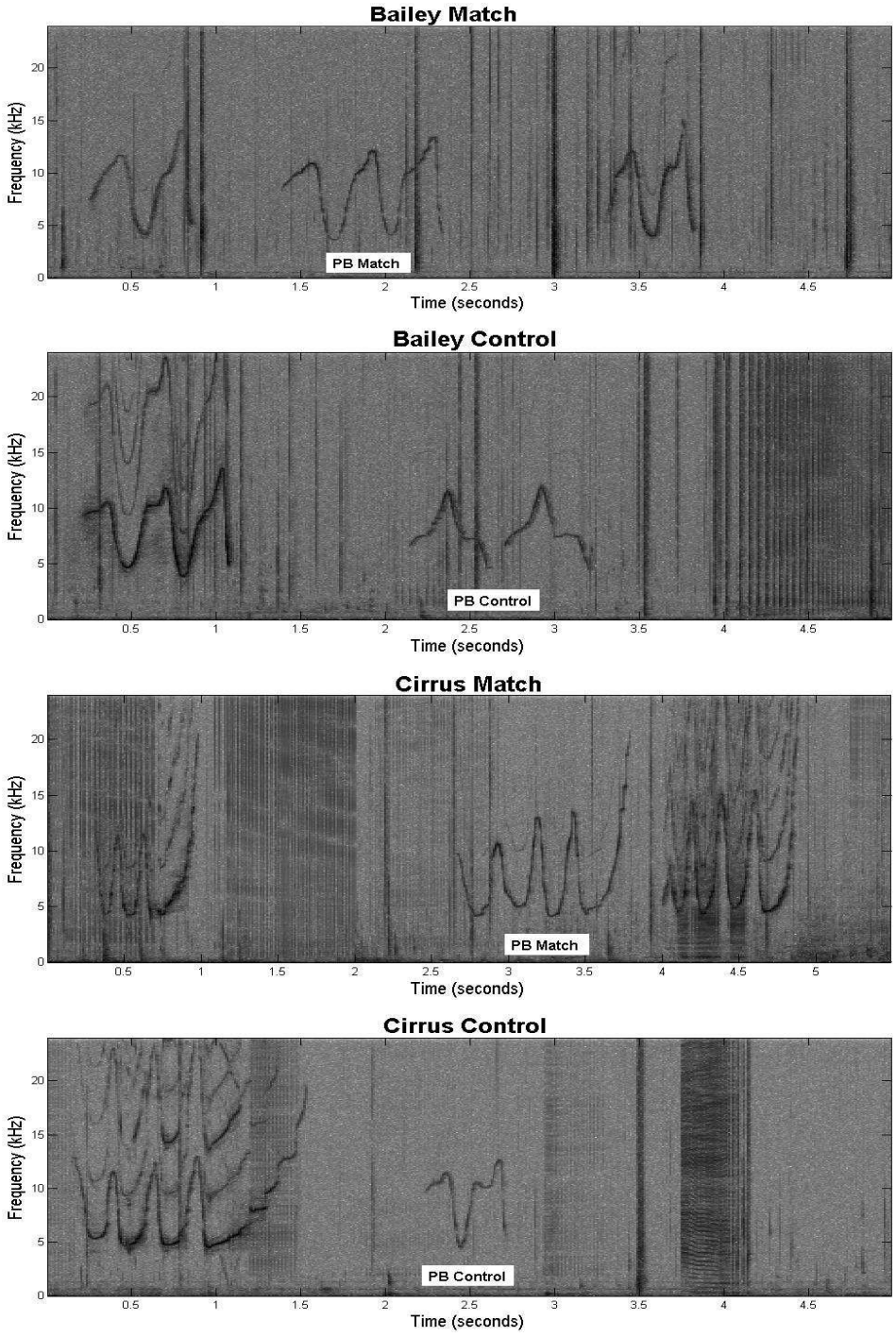

Figure 3.4b. Spectrograms showing an example of a matching playback and then a control playback for each of the adult females respectively (Bailey and Cirrus): sampling rate is 48000 Hz, FFT length 1024, Hanning window function. The playback stimuli are highlighted with the label "PB".

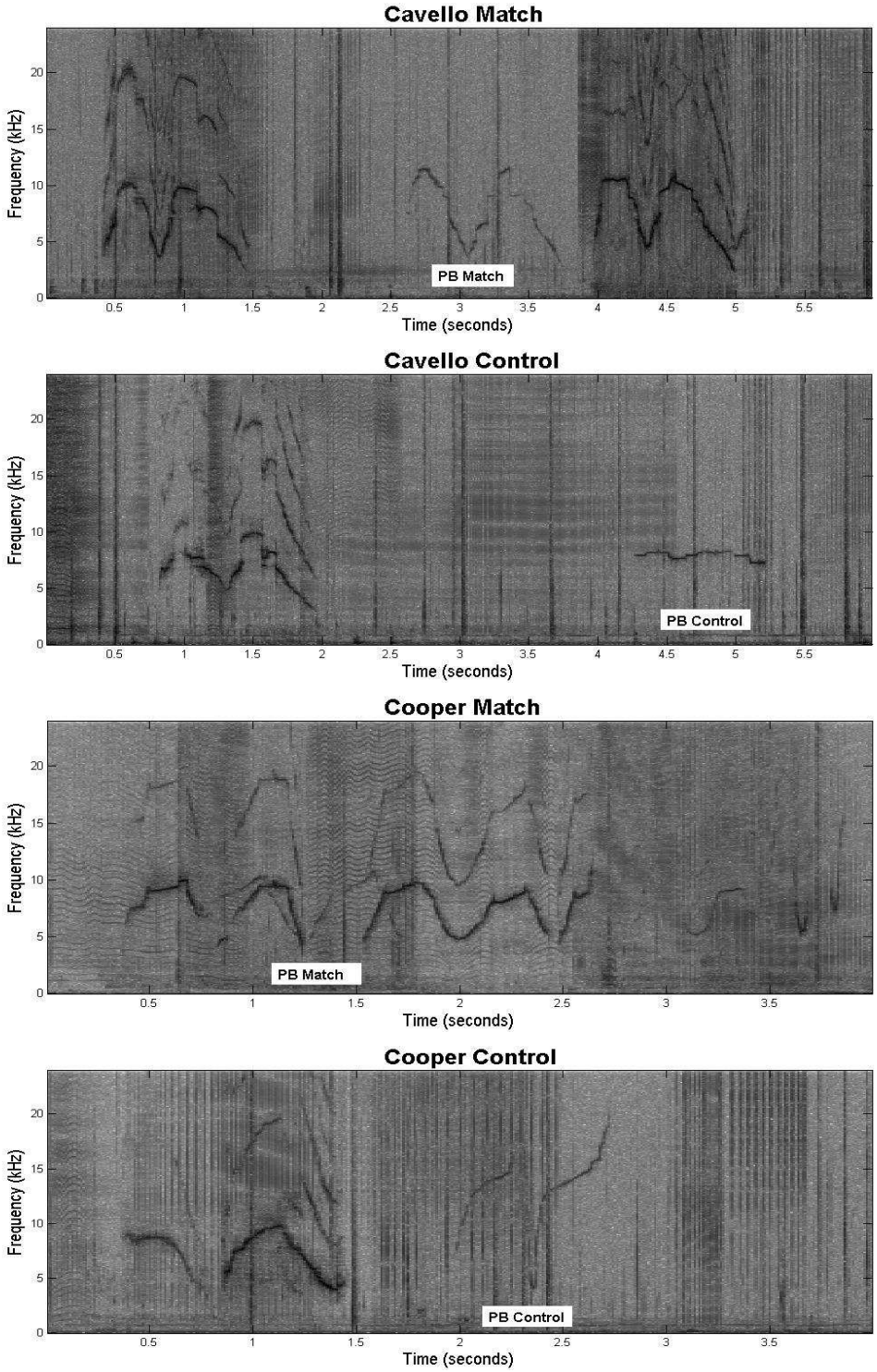

Figure 3.4c. Spectrograms showing an example of a matching playback and then a control playback for each of the calves respectively (Cavello and Cooper): sampling rate is 48000 Hz, FFT length 1024, Hanning window function. The playback stimuli are highlighted with the label "PB".

There was a significant decrease in vocal response ($P < 0.02$) as time between the animal vocalizing and the playback increased (Table 3.2). Further examination revealed there was a clear pattern with the animal nearly always responding to a playback of its own signature whistle (match) when it occurred within 1 second after the animal vocalised (see Figure 3.5). The average latency between the playback match and the animal's response was 0.53 seconds (range from 0.01 to 1.8) for The Seas and 0.8 seconds (range from 0.2 to 5) for Dolphin Quest. There was also a slight increase in vocal responses to the playbacks of a different signature whistles (control) within the same time period. There seems to be an optimum time frame in which a match should occur (< 1 second), above which there is a decline in response strength.

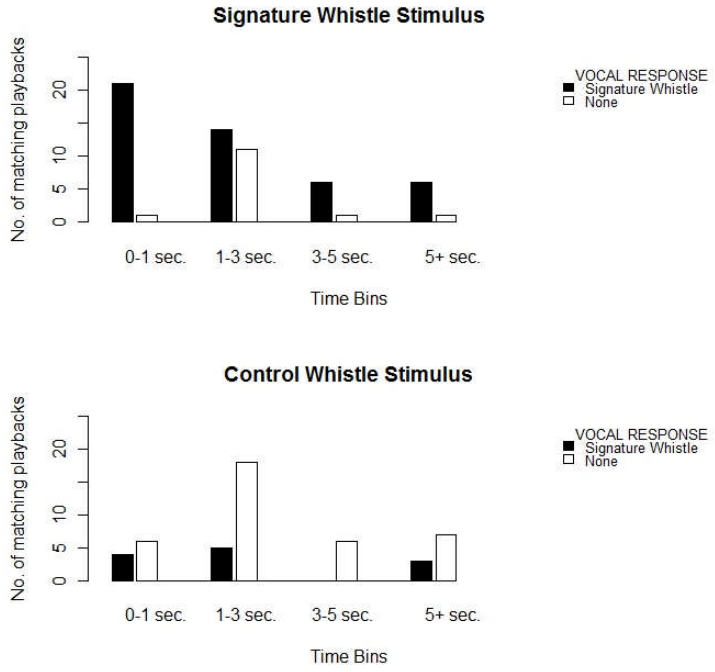

Figure 3.5. The vocal response of 7 target animals to being vocally matched by either their own signature whistle (top) or a different signature whistle (bottom) at varying lengths of time after they produced their own signature whistle. The vocal response is either the target animal producing its signature whistle (black) or there was no response or another vocalisation (white).

The control playbacks (different signature whistles) were comprised of both familiar and unfamiliar signature whistles. The animals might not show a strong vocal response to the unfamiliar signature whistles purely because the whistles were unfamiliar to them. This was addressed by also using familiar signature whistles of non-target animals from the same facility as the target animal. These familiar signature whistle controls were incorporated for a total of 11 playbacks to 3 different animals (1 from The Seas; 2 from Dolphin Quest). No difference was found in the responses given to the two types of different signature whistles used as controls (Fisher's exact test: N = 50, P = 1), see Figure 3.6.

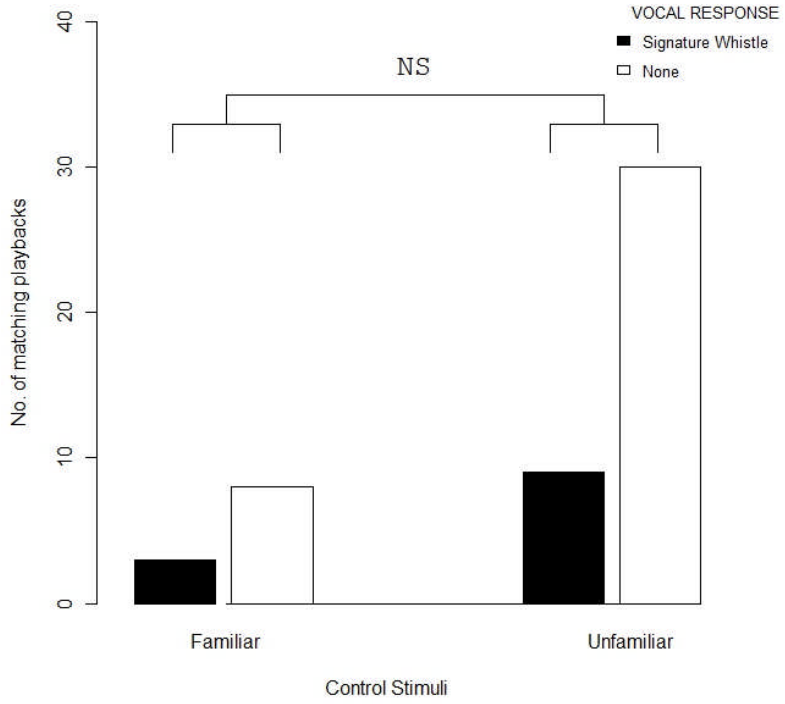

Figure 3.6. The vocal response of 3 captive bottlenose dolphins to the control playbacks comprising signature whistles of pool mates (familiar) and signature whistles of unknown wild or captive animals (unfamiliar). The vocal response can either be the animal producing its signature whistle (black) or there was no response or another vocalization (white).

3.3.2 Do animals adjust acoustic parameters of their signature whistle as a result of being matched?

There was no evidence that the animals were adjusting the acoustic parameters of their signature whistles as a result of being vocally matched (see Table 3.3). Only 4 out of the 7 animals were included in this analysis due to small sample sizes. They were therefore not adjusting their signature whistle to more closely match or deviate from the playback whistle.

Table 3.3. Frequency and temporal parameters of the signature whistles of 4 animals before and after the match playback. An F test was used to compare variances followed by a paired t test with a Bonferroni--adjusted significance level of $p < 0.002$

	N	Before Playback	After Playback	P
		Mean ± SD	***Mean ± SD***	
No. of Loops				
- Ranier	17	2.2 ± 0.2	1.9 ± 0.2	0.2
- Khyber	4	2.2 ± 0.9	2.7 ± 0.9	0.1
- Cirrus	16	2.7 ± 0.7	2.8 ± 0.5	0.8
- Bailey	6	1.8 ± 0.4	1.4 ± 0.5	0.3
Start Freq. (kHz)				
- Ranier	17	5.3 ± 0.4	4.4 ± 0.2	0.08
- Khyber	4	9.8 ± 0.9	9.4 ± 1.8	0.7
- Cirrus	16	7.9 ± 3.3	7.2 ± 2.7	0.4
- Bailey	6	4.9 ± 0.6	11.9 ± 7.1	0.08
End Freq. (kHz)				
- Ranier	17	21.4 ± 1.1	22.1 ± 0.6	0.5
- Khyber	4	6.8 ± 0.9	7.4 ± 0.3	0.2
- Cirrus	16	21.9 ± 3.2	23.2 ± 4.7	0.2
- Bailey	6	12.8 ± 1.2	15.6 ± 3.8	0.2
Minimum Freq. (kHz)				
- Ranier	17	4.0 ± 0.2	3.8 ± 0.2	0.2
- Khyber	4	6.8 ± 0.9	6.7 ± 0.7	0.8
- Cirrus	16	4.3 ± 0.4	4.2 ± 0.3	0.8
- Bailey	6	4.3 ± 0.6	5.6 ± 2.0	0.2
Maximum Freq. (kHz)				
- Ranier	17	21.4 ± 1.1	22.1 ± 0.6	0.5
- Khyber	4	13.0 ± 0.8	13.5 ± 0.7	0.06
- Cirrus	16	22.0 ± 3.2	23.4 ± 4.5	0.2
- Bailey	6	4.0 ± 0.07	4.4 ± 0.6	0.2
Duration (secs.)				
- Ranier	17	0.5 ± 0.04	0.4 ± 0.03	0.06
- Khyber	4	0.7 ± 0.3	0.8 ± 0.3	0.1
- Cirrus	16	0.9 ± 0.2	0.8 ± 0.1	0.1
- Bailey	6	0.8 ± 0.2	0.6 ± 0.2	0.03

3.3.3 Do animals adjust their behaviour in response to being vocally matched?

The behavioral responses of 6 target animals to the matching playbacks (n=35) and the control playbacks (n=27) were analyzed. Animals did not respond differently to the two playback treatments (see Table 3.4, Figure 3.7).

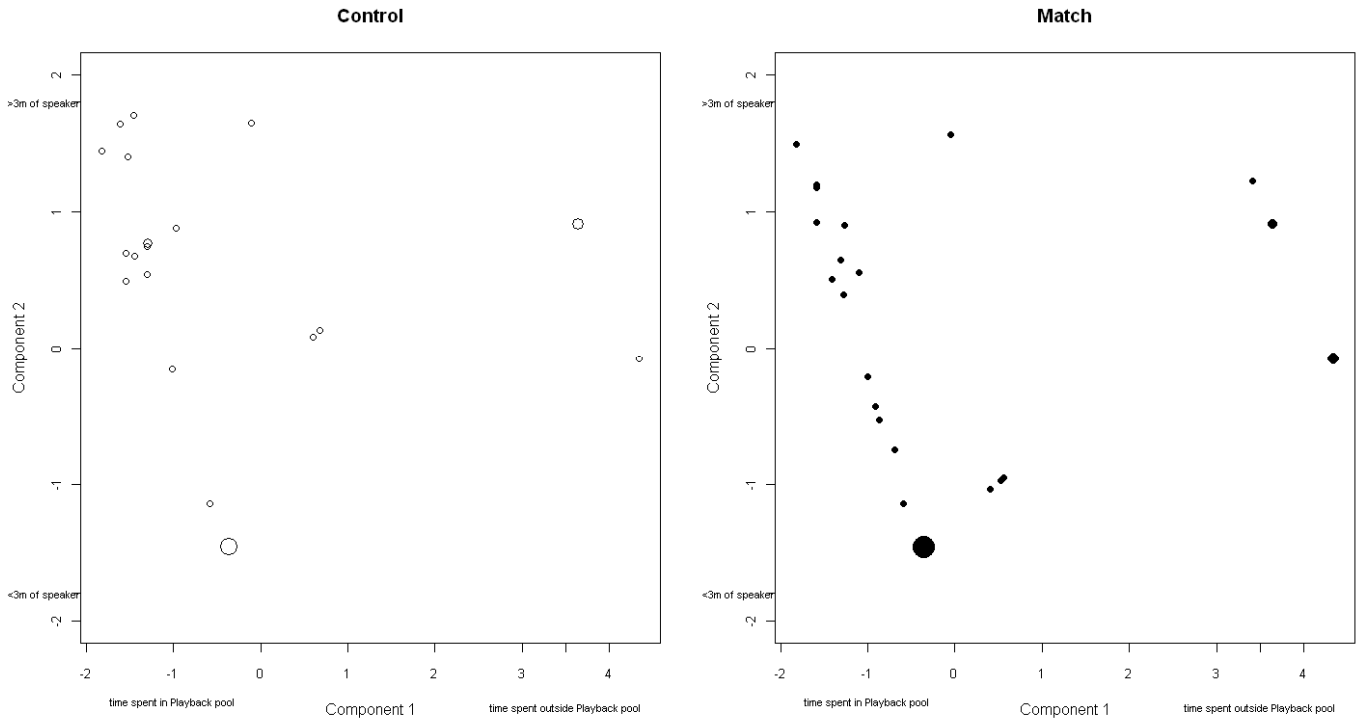

Figure 3.7. A reduced space plot of the principal component scores of the behavioural response of 6 target animals 1 minute after the playback treatments; own signature whistle (match) (black) n=35, and different signature whistle (control) (white) n=27. Larger circles represent multiple points at those co-ordinates.

Table 3.4. The behavioural response to the two playback treatments by 6 animals; different signature whistles (control, n=27) and own signature whistle (match, n=35). The principal component scores (Mean ± SE) for the first two components are given, the P value is for a two-tailed Wilcoxon rank sum test with a Bonferroni--adjusted significance level of $p < 0.025$.

	Playback Treatment		
	Control		Match
PC score			
Component 1	-0.17 ± 0.35		0.13 ± 0.32
P value		0.3	
Component 2	0.23 ± 0.19		-0.18 ± 0.19
P value		0.2	

The variation is described by which pool the animal spent the most time in (component 1: Wilcoxon rank sum test: W = 400, P = 0.3) and the distance to the speaker (component 2: Wilcoxon rank sum test: W = 562, P = 0.2). I found no presence of behavioural reactions aligned with aggressive behaviour such as jaw popping, tail slapping or repeated emission of intense, loud vocalisations.

3.4 Discussion

Whistle matching in dolphins has been discussed as being indicative of animals addressing each other individually (Janik 2000; Tyack 1991). An animal may address a social companion by copying its signature whistle and producing it in a vocal matching event. Vocal matching can be used as a tool to initiate contact with the signature owner, by replying to the signature quickly after the owner produces it. It allows the receiver to direct a response towards the signaler and facilitate a short-term communication channel between them. The idea that vocal matching is used to address individuals would be supported if there was a reliable vocal response to being matched. This work has shown that bottlenose dolphins do produce a consistent vocal response to being vocally matched, by returning the match (Figure 3.1), with no associated signal of aggression. The matching of signature whistles therefore can be seen to play an important role in addressing individuals in the dolphin communication system.

In addition, this work provides evidence that the timing of the match mediates response strength (Table 3.2, Figure 3.3). There is an optimum time delay (< 1 second) in which a match should occur in order to elicit an immediate interaction with the signaler. If the playback was transmitted later than this there was a decline in response strength. This result fits with those of Nakahara & Miyazaki (2011) who showed that counter-calling between two bottlenose dolphins occurs in < 1 second time periods. If an animal calls often it may call 1-2 seconds after another animal by chance alone, but calling immediately after another animal is much less likely to be a coincidence. The tight temporal sequencing of vocal interactions allows animals to discern between a reply and an independent call.

Overall it seems that a dolphin may vocally match another dolphin's individually distinctive signature whistle in order to establish responsive calling with that animal. In the fission fusion society of the bottlenose dolphin, where there is fluid group movement, individual

recognition appears to have been heavily selected for (Sayigh et al., 1999). Bottlenose dolphins have a large social network with high encounter rates with one another (Connor et al., 2000), and although they have excellent vision this is restricted in an underwater environment. Selective pressure has instead been placed on the development of learned, unique vocal signatures that facilitate recognition (Tibbetts & Dale 2007). Each dolphin produces one signature whistle type which can form a minor part of another animal's repertoire as a result of copying, but it only forms a major part of one animal's repertoire, allowing it to be a vocal label for that particular individual. It is therefore likely that vocal matching functions in mediating a vocal interaction between two specific individuals.

Vocal matching has an agonistic role in some male songbirds where it can occur between both territorial neighbours and strangers. Both males however must share at least some of their song repertoire in order to vocally match one another (Searcy & Beecher 2009). Male songbirds may identify one another by becoming familiar with each other's song repertoire via location of territories or fine-scale differences between individuals in shared song types. This contrasts to bottlenose dolphins that use a single, learned signature whistle as a signal of identity (Caldwell & Caldwell 1965; Caldwell et al., 1990; Janik et al., 2006). Signature whistle matching can only occur if an animal copies the signature whistle of another animal. Dolphins can copy novel acoustic signals after only one exposure (Richards et al., 1984), and therefore are likely able to copy the signature whistle of a stranger. So far, however, signature whistle copying has been shown to occur amongst closely-bonded animals, and these copies may even contain information on the copier's identity (Chapter 5). Thus, in contrast to birds, it may be unlikely that strangers would match signature whistles in the bottlenose dolphin communication system. However, their ability to imitate a signal after only one exposure (Richards et al. 1984) means that unlike songbirds (who have to share the song type in order to match), dolphins could match complete strangers.

Animals did not seem to adjust fine scale parameters of their signature whistles as a result of being matched (Table 3.3). It therefore seems unlikely that additional information is encoded within the whistle pertaining to the animal's motivational state, but rather the response in itself is strong indication of the animal's motivation to communicate.

In addition, no differences were found in the behaviour of the target animals between the two playback treatments. Many of the playback animals approached the speaker and stayed within 3 metres of it (Figure 3.5). A key measure of aggressive response in song birds is close approach and continued proximity to the speaker (Beecher et al., 2000; Krebs et al., 1981; Mcgregor et al., 1983). Bottlenose dolphins, however, are not territorial and are not under the same social pressures as songbirds. The close approach or continued proximity of conspecifics is not a known sign of aggression in the bottlenose dolphin communication system. Instead aggression is aligned with other signals such as an increase production of burst-pulsed sounds, jaw popping (Overstrom 1983) or increased swim speed (in captive animals). The subjects in this study showed high levels of interest to the playback speaker, irrespective of playback type, but with no evidence that playback induced aggressive states.

Vocal matching with signature whistle types is not, therefore, aligned with aggression analogous to song type matching in song sparrows. This result is aligned with another study (Chapter 5). In songbirds an individual may respond to being matched by singing the same song type and reciprocating the match. In this instance the aggressive connotation of the interaction is escalated (Searcy & Beecher 2009). The bottlenose dolphin instead nearly always replies to being matched by calling back with the same call (its own signature whistle) and this is true for adult males, adult females and young calves. As such it is unlikely that reciprocating the match in dolphins has an agonistic role. Instead a more affiliative function is supported, such as the strengthening or mediating of social relationships, or facilitating localisation within groups of

animals. The identification of individuals is greatly enhanced by their highly individualized signature whistles. The matching of these whistles, whereby a vocal response is reliably elicited, allows animals to localise or initiate interactions with other individuals they specifically want to associate with.

This study has shown that vocal matching between a pair of animals may function as an effective mechanism of addressing one another. Whistle matching, however, may also occur between three or more animals (Janik 2000). This suggests it may play a role in communicating information between groups of animals, and that its function may be multi-faceted.

Bird song has long been acknowledged as an influential model system to address evolutionary questions on vocal learning and complex vocal communication (Catchpole & Slater 2008). Vocal learning is discussed as a pre-requisite for the evolution of spoken language (Fitch 2005). It is important in both the development of birdsong (Catchpole & Slater 2008) and in the ontogeny of signature whistles which are developed within the first year of life (Fripp et al., 2005; Miksis et al. 2002; Tyack & Sayigh 1997). Interestingly, both species are also highly sophisticated at vocal imitation (Catchpole & Slater 2008; Richards et al. 1984). This study has shown, as with songbirds, bottlenose dolphins can use their learned calls in vocal matching interactions to address specific individuals. In bottlenose dolphins, vocal matching appears to be an affiliative signal between closely bonded animals; in songbirds vocal matching is a signal of aggressive intent between male territory holders. Nevertheless, species from two different taxa, which are under completely different selective pressures, have converged on a similar mechanism to address individual conspecifics using learned signals. The copying of learned signals, as a way of addressing social companions, is ubiquitous in human society. The striking parallel between nonhuman taxa presented here can therefore provide a significant contribution to our understanding of the roots of human language evolution.

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Chapter 4

The rapid matching of whistle types correlates with foraging behaviour in the bottlenose dolphin (*Tursiops truncatus*)

4.1 Introduction

Foraging behaviour and social complexity have been discussed as causative factors for the evolution of intelligence. Social animals that show complex cognitive skills in the form of tool manufacture and/or use as a form of foraging behaviour; such as primates, cetaceans, and corvids are widely regarded as of superior intelligence to other animal species (Emery & Clayton, 2004). Highly social delphinids use diverse foraging techniques, some involving complex social behaviour. Bottlenose dolphins are known to utilise a number of foraging techniques; these include sponge feeding as a form of tool use (Krützen et al., 2005; Smolker et al., 1997); the synchronised pursuit of prey onto mud banks (Hoese, 1971; Rigley, 1983); the formation of cooperative feeding associations with humans (Pryor et al., 1990); and role specialisation of individuals during group foraging (Gazda et al., 2005).

A number of these techniques may require that animals are able to track one another's movements. Animals that live in close-knit groups can coordinate behaviours through the use of acoustic cues. For example, female greater spear-nosed bats (*Phyllostomus hastatus*) use broadband calls to coordinate foraging movements (Wilkinson & Boughman, 1998), and vocal calls are used to coordinate group movement in both white-faced capuchins (*Cebus capucinus*) (Boinski, 1993) and green woodhoopoes (*Phoeniculus purpureus*) (Radford 2004). The pied babbler (*Turdoides bicolor*) gives a short call known as a 'close' call during foraging

behaviours, functioning as a contact call and maintaining group cohesion (Radford & Ridley 2008).

These acoustic signals can occur in tightly timed vocal exchanges, and this matching of acoustic signals may be particularly suited for allowing conspecifics to exchange information on their distance (Falls et al., 1982; Krebs et al., 1981). The matching of call types as a way of locating group members and maintaining within-group contact occurs in a number of social species, including primates (Sugiura, 1998); odontocetes (Miller et al., 2004; Schulz et al., 2008; Janik 2000b); and bats (Jones & Ransome, 1993). The matching of calls is useful because it firstly allows animals to direct a response towards an intended receiver (Bremond, 1968; Janik, 2000a; Krebs et al., 1981) and secondly, it allows animals to exchange information on their distance from one another (see section 2.1.4 in Chapter 2).

It makes sense in an underwater environment, where vision is restricted, that animals use acoustic signals. The use of vocalisations during foraging behaviour may be advantageous for multiple reasons. It may allow animals to maintain contact with one another, attract conspecifics to a food source, allow animals to manipulate prey behaviour, or facilitate coordinated foraging (Janik 2009). A number of mechanisms may be available for animals to coordinate such behaviours. Dolphins may maintain tight group formation in order to eavesdrop on one another's echolocation clicks (Götz et al., 2006), allowing them to coordinate movement. However, when animals are dispersed over a larger spatial scale then other acoustic cues may be required. Bottlenose dolphins have large communication networks and can classify individual animals by their individually specific signature whistles. The development of signature whistles is influenced by vocal learning (Fripp et al., 2005; Miksis et al., 2002; Tyack & Sayigh, 1997). Playback experiments have revealed that signature whistle shape, or contour pattern, carries identity information irrespective of voice features (Sayigh et al., 1999; Janik et al., 2006). Bottlenose dolphins exchange signature whistles when meeting in the wild (Quick & Janik, 2012), and use the alternation of signature whistles

to locate conspecifics when isolated and for group cohesion (Tyack 1986; Caldwell et al., 1990; Janik & Slater 1998; Nakahara & Miyazaki 2011; Smolker et al., 1993).

Signature whistles can also be copied by conspecifics (Tyack 1986; Janik & Slater 1998; Janik 2000b). Thus, bottlenose dolphins may maintain spatial formation by exchanging information on their distance from one another by copying one another's signature whistles. This may be more effective than individuals calling their own signature whistles because matching allows an individual to direct a call to an intended receiver (Bremond, 1968; Janik, 2000a; Krebs et al., 1981). Information can then be directly shared between specific individuals.

Call-type matching is used by killer whales (*Orcinus orca*) to coordinate group movement during foraging and travelling (Miller et al., 2004). This matching of social calls may convey reliable information about distance of both the signaller and receiver, known as '*the distance signalling hypothesis'* (Krebs et al., 1981; Falls et al., 1982; Morton 1982; Todt & Naguib 2000). Janik has shown that wild, unrestrained bottlenose dolphins will vocally match one another (Janik 2000b). Interestingly, matching interactions were most frequent when group size was greater than ten, and most interactions involved two animals, where each produced a single whistle. In mobile species, such as the bottlenose dolphin, group cohesion, the acoustic range of group members and co-operative aspects of foraging behaviour may be maintained by sound source localization (Miller, 2002). Animals may make more efficient decisions with regards to speed and direction of movement if they are able to maintain acoustic contact during co-ordinated foraging behaviours (Miller, 2002). Therefore, in line with the '*distance signalling hypothesis*', bottlenose dolphins may use vocal matching to range individuals, which may promote certain behaviours such as cooperative foraging.

In the Moray Firth, Scotland, bottlenose dolphins produce a low-frequency, burst-pulsed sound called a bray (dos Santos et al., 1995; Janik 2000a). Brays calls are usually produced in bouts by one dolphin (Janik 2000a). They are believed to facilitate prey capture

by exploiting the perceptual system of the prey and were produced in 93% of observed feeding events by Janik (2000a). A by-product of this call production is the fast approach of conspecifics to the area. Bray calls are produced at depth (20m – 30m), with animals diving to depth prior to the bray and returning to the surface immediately after (Hastie et al., 2005).

In order to discern whether vocal matching plays a role in foraging behaviour I investigated the use of narrow-band, frequency modulated whistles in the context of bray call production. I use bray calls as a proxy for foraging behaviour, because all cases of bray production were closely associated with dolphins at the surface with large fish (Hastie et al., 2005). If animals wish to maintain spatial formation during foraging events then the matching of whistle types may be expected to occur in close proximity to bray calls. I conducted focal follows on groups of wild animals during the summer months when Atlantic salmon (*Salmo salar*) is most abundant, in line with previous studies (Janik 2000a; Hastie et al., 2005). I was unable to localise whistles to individuals with the recording system. I therefore used overlapped whistles of the same type as a conservative measure for whistle matching, where I could be sure that at least two animals were vocalising. If whistle matching plays a role in foraging behaviour I expect it to occur in tight temporal proximity to the production of brays.

4.2 Methods

4.2.1 Data Collection

The study was conducted in St Andrews Bay off the north-east coast of Scotland between Montrose and Fifeness during May and September 2010. During this period a resident population of approximately 130 bottlenose dolphins are frequently sighted, who range from the Moray Firth to St Andrews Bay (Wilson et al., 1999; Wilson et al., 2004). Group follows

were conducted upon a small 6m boat at sea state 3 or less. Once a focal group was chosen photo-identification was carried out with a Canon Digital 30D SLR camera with a Sigma 100-300mm, F4 zoom lens. If group composition changed with ≥ 1 animal(s) either leaving or joining the group then spacer photographs were taken and the group was re-photographed. The focal group was tracked closely and all other animals in the area were noted.

Acoustic recordings of the focal group were taken using two HTI-96 MIN hydrophones (frequency response: 0.002 to 30 kHz ±1 dB) towed at 2m depth. Recordings were made on a Toshiba Satellite Pro Laptop using an Edirol UA-25 with a sampling rate of 96000 Hz, 16 bit.

4.2.2 Identifying Vocal Matches

The acoustic recordings were analysed by inspecting the spectrograms (FFT length 1024, 87.5% overlap, Hanning window) in Adobe Audition v2.0 (Adobe Systems). All statistical procedures were conducted in R (R project for statistical computing; GNU project).

Recordings were screened by eye for occurrences of low-frequency bray calls and frequency modulated whistles. Those recording segments where engine noise exceeded 2 kHz were discarded from the analysis. Bray calls were identified by their low frequency pulse followed by a short downsweep (Janik 2000a; dos Santos et al., 1995). Brays calls are usually produced in bouts (Janik 2000a) and therefore a series of brays in close proximity are treated as one braying event (Figure 4.1).

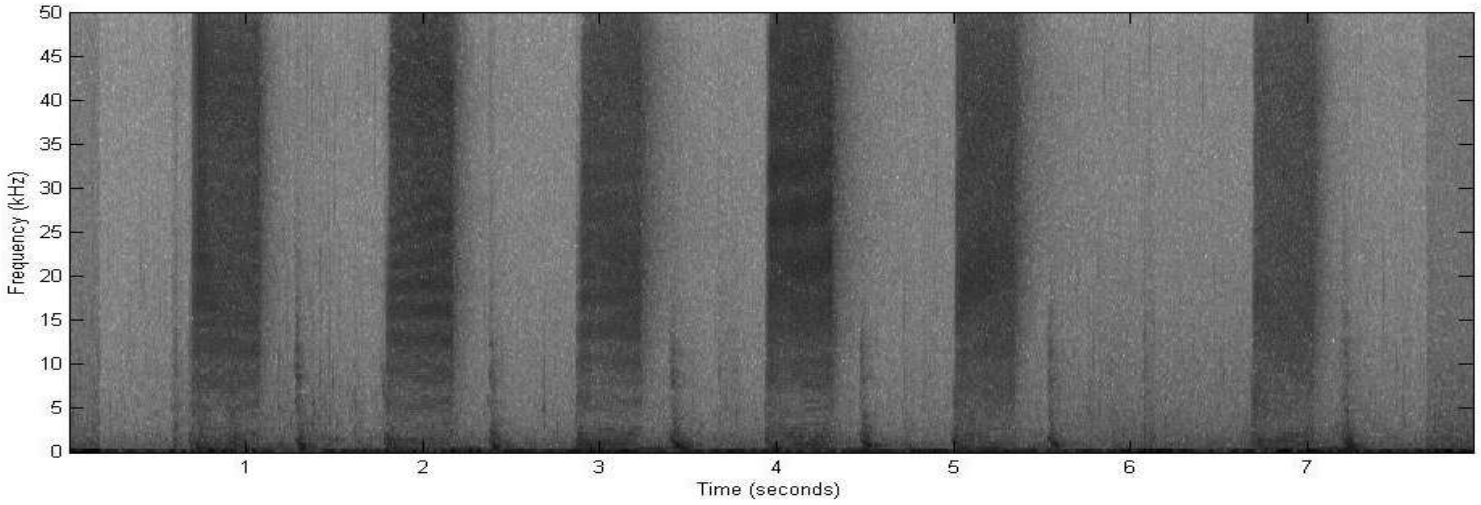

Figure 4.1 Brays. A braying bout with a sampling rate of 100 kHz, FFT 2048, Hanning window function, and 100% overlap between FFT.

I identified all occurrences of the same whistle contour pattern being produced in an overlap match sequence interaction by inspecting spectrograms.

The distance of the vocalising animals to the boat will affect whether a true overlap match has occurred. For example, in figure 4.2a, the whistles overlap by 0.11 seconds (110 milliseconds). Given a speed of sound in water of approximately 1500 metres per second, the animals therefore had to be ≤ 165m apart to truly overlap. However, if animals are within a 90 degree arc of each other in relation to the boat they could be > 165m apart from one another but both within 165m of the recording vessel. In this case the apparent overlap could result from the recording position. Ultimately this discrepancy is not important as I am using overlap matching as a proxy for two different animals producing the same whistle type within a short time window, which is the case for both scenarios.

There is, however, one whistle type missing from the analysis, which is non-overlap matching. One way to address this would have been to classify same whistle types that occurred within 3 seconds (Janik, 2000a) of each other as a non-overlap match. A major flaw with this approach, however, is that bottlenose dolphins produce their signature whistles in

repetitive sequences with inter-whistle intervals commonly between 1 – 10 seconds (Janik et al., 2012). This means that the same whistle types commonly occur in close temporal proximity to one another but are normally produced by the same animal. Incorporating non-overlap match as a category would result in elevated numbers of false positive vocal matches. This stems from the lack of ability to localise whistles to the individual as used in other studies (Janik, 2000a). Instead I use overlap matching as a conservative measure of whistle matching.

Whistles were categorised into one of three sequence types (Table 4.1).

Table 4.1. Definitions of the three different categories of whistle types used in the analysis.

Whistle Type		Definition
(1)	overlap match	the same whistle type is produced in a sequence where two or more whistles overlap one another.
(2)	overlap no match	the overlapping of different whistle types.
(3)	no overlap, no match	non overlapping whistle sequences of the same or different whistle types.

An overlap match was defined as two whistles of the same contour pattern (change of frequency over time) where the end point of one whistle finished after the start of the other whistle (Figure 4.2a-c). Whistles could either be continuous in their frequency contour pattern or they could be multi-loop whistles. Multi-loop whistles were defined as a repeated modulation pattern that could be separated by periods of stereotyped silence up to 250ms in length (Esch et al., 2009). As such, whistles with periods of silence of less than 250ms were treated as the same whistle (Figure 4.2c).

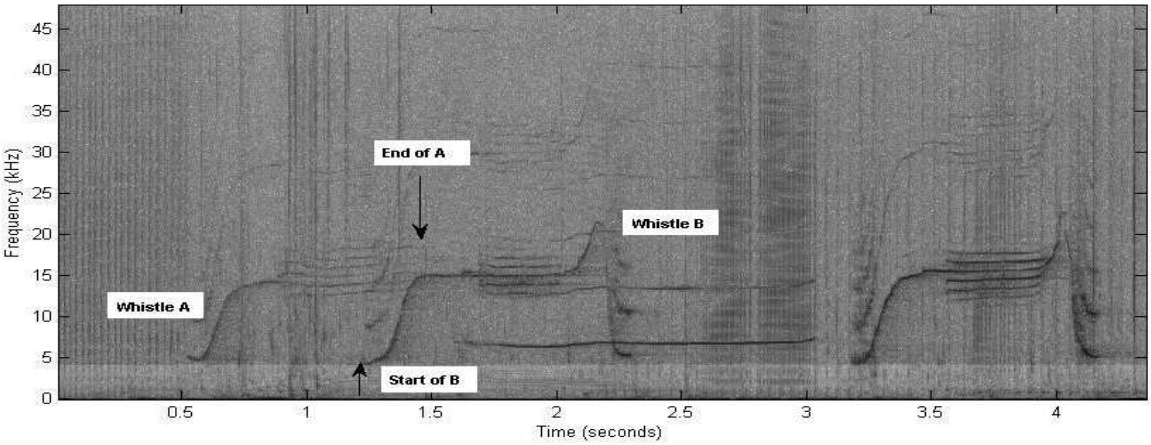

Figure 4.2a. An example of an overlap match, where two whistles of the same type overlap in time. The end of whistle A occurs after the start of whistle B.

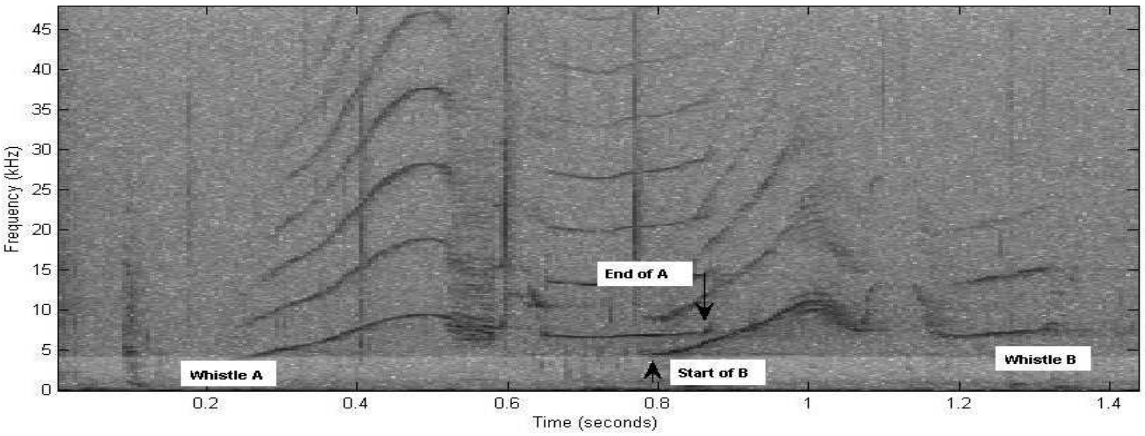

Figure 4.2b. Example of an overlap match, where two whistles of the same type overlap in time. The end of whistle A occurs after the start of whistle B.

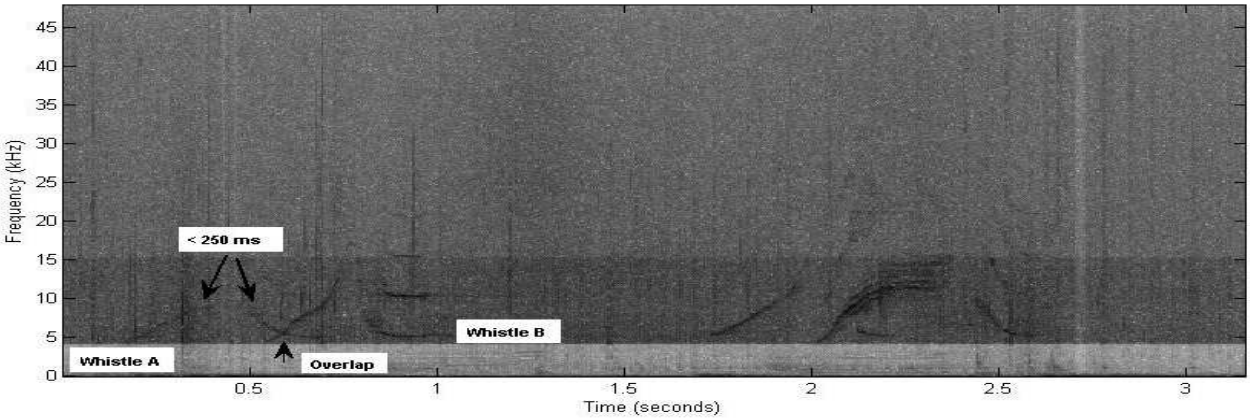

Figure 4.2c. Example of an overlap match, where two whistles of the same type overlap in time. The end of whistle A occurs after the start of whistle B. Whistle A has a period of interrupted silence, this silence is < 250ms and therefore the whistle is treated as one whistle in spite of the short gap.

The most common interval between signature whistles of the same type is 5 – 10 seconds (Janik et al. in press). Therefore, a cut off interval of 5 seconds was used to separate different whistle types, and 10 seconds was used as a cut off interval for the same whistle types. For example, if consecutive whistles had an inter-whistle interval of 5 seconds or less they were grouped together into one bout for that sequence type and the start and end time of that bout was noted. If 4 whistles of the same type were produced with an inter-whistle interval of ≤ 5 and 2 were overlapping, the whole bout was considered a Type 1 (overlap match), and the start and end time was noted (see Figure 4.3 and Figure 4.4a).

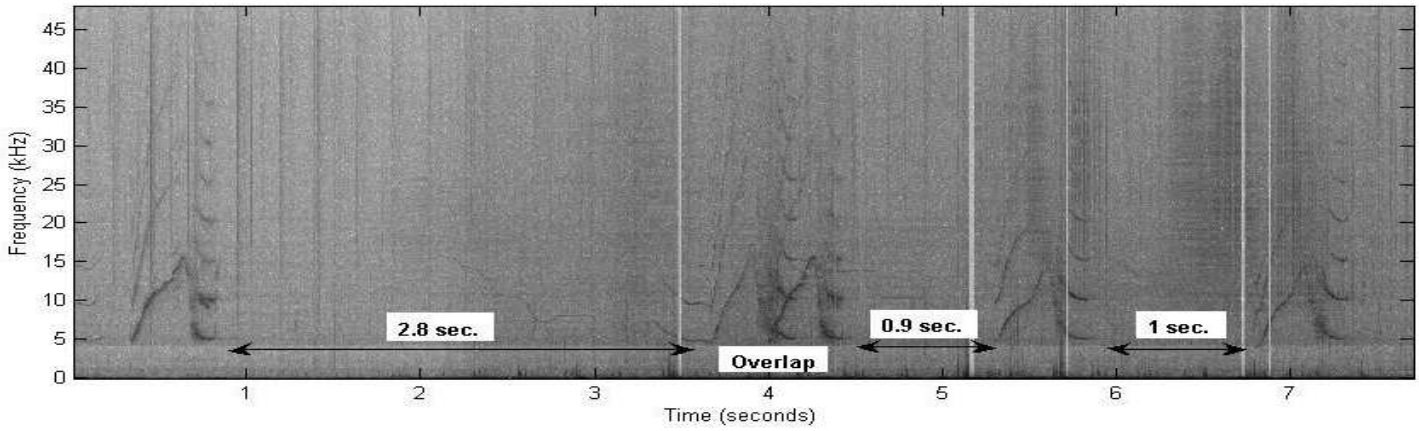

Figure 4.3. A sequence of whistles grouped together into an overlap match, where the inter-whistle intervals are all < 5 seconds.

If the same whistle type was produced in a repetitive sequence with inter-whistle intervals of 10 seconds or less, and no overlap, it was treated as one case of no overlap, no match. Signature whistles are stereotyped whistles that are produced in sequences with inter-whistle intervals of 1-10 seconds (Janik et al., in press). The cut off interval of 10 seconds for same type whistles allows the grouping of a signature whistle bout into one emittance. A shorter interval was used for different whistle types as a conservative measure.

A total of 23 hours and 51 minutes of recordings were analysed spanning 18 days from June to August 2010, of which only 12 hours and 08 minutes from 15 days were of sufficient sound quality for further analysis. Low-frequency bray calls were present in 11 hours and 6 minutes of recordings taken from 11 of the 15 different days between June and August. Photo-ID effort was analysed for 8 of the 15 days used in the analysis. A total of 62 individual animals were identified with 56% sighted just once, 22% were sighted on two different recording days, and 21% were sighted on multiple recording days. The average re-sighting for a given individual was 1.85 (range: 1-6). Average group size per encounter was 10 animals (range: 3-23).

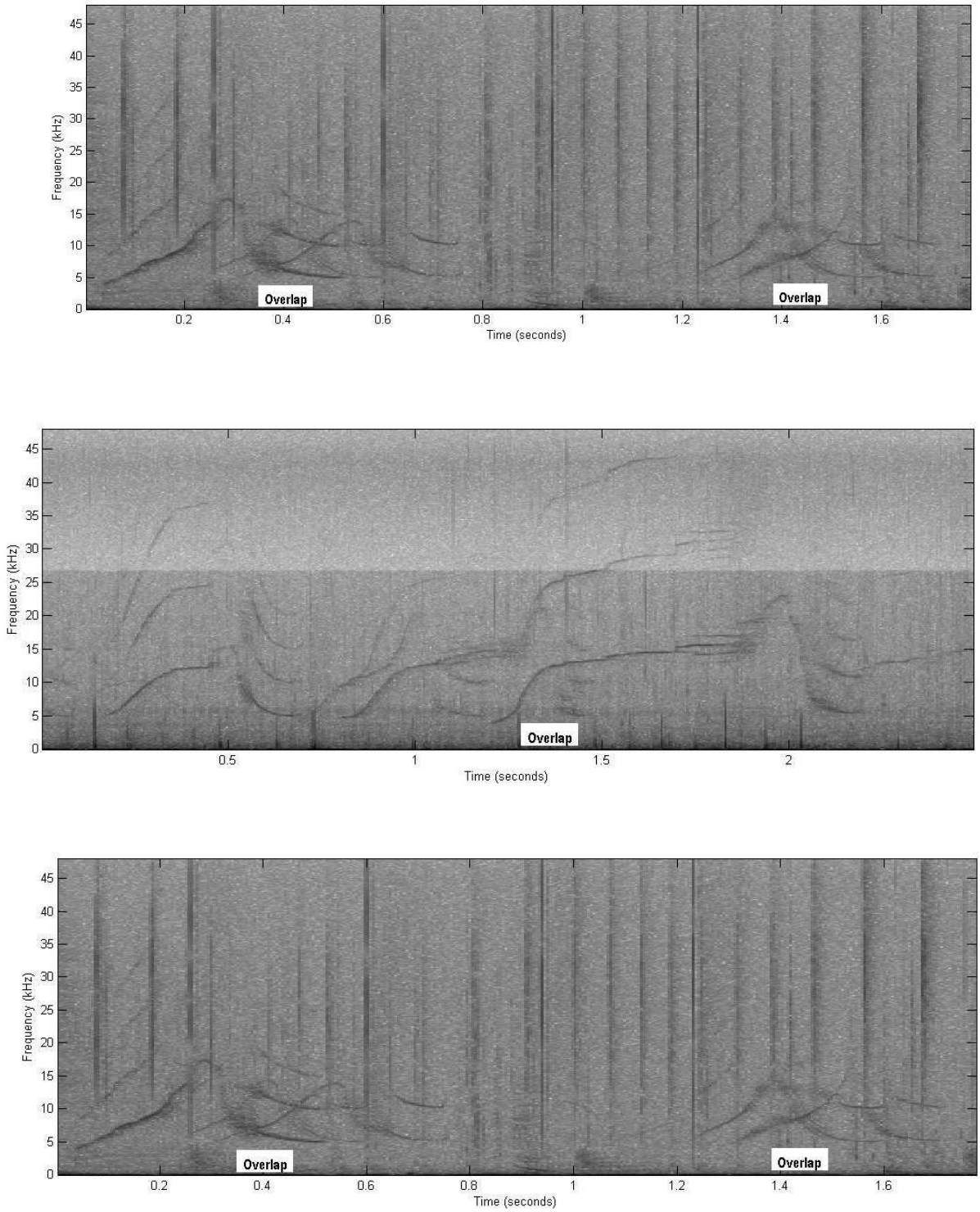

Figure 4.4a. Overlap Matches: Examples of overlap match whistle sequences where the same whistle type is produced in an overlapping sequence. The sampling rate is 100 kHz, FFT 2048, Hanning window function, and 100% overlap between FFT.

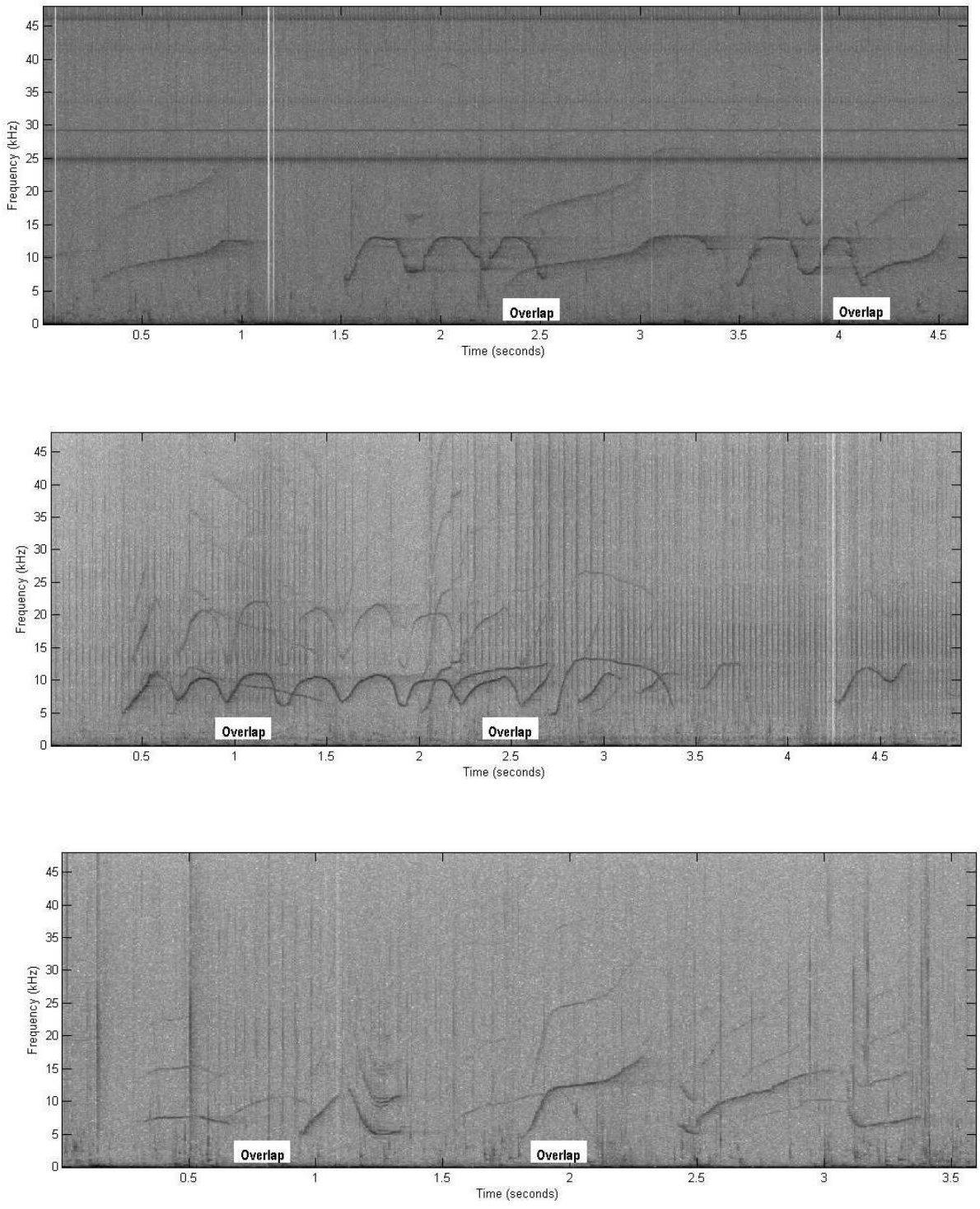

Figure 4.4b. Overlap Non Matches. Examples of overlap no match whistle sequences where different whistle types are produced in an overlapping sequence. The sampling rate is 100 kHz, FFT 2048, Hanning window function, and 100% overlap between FFT.

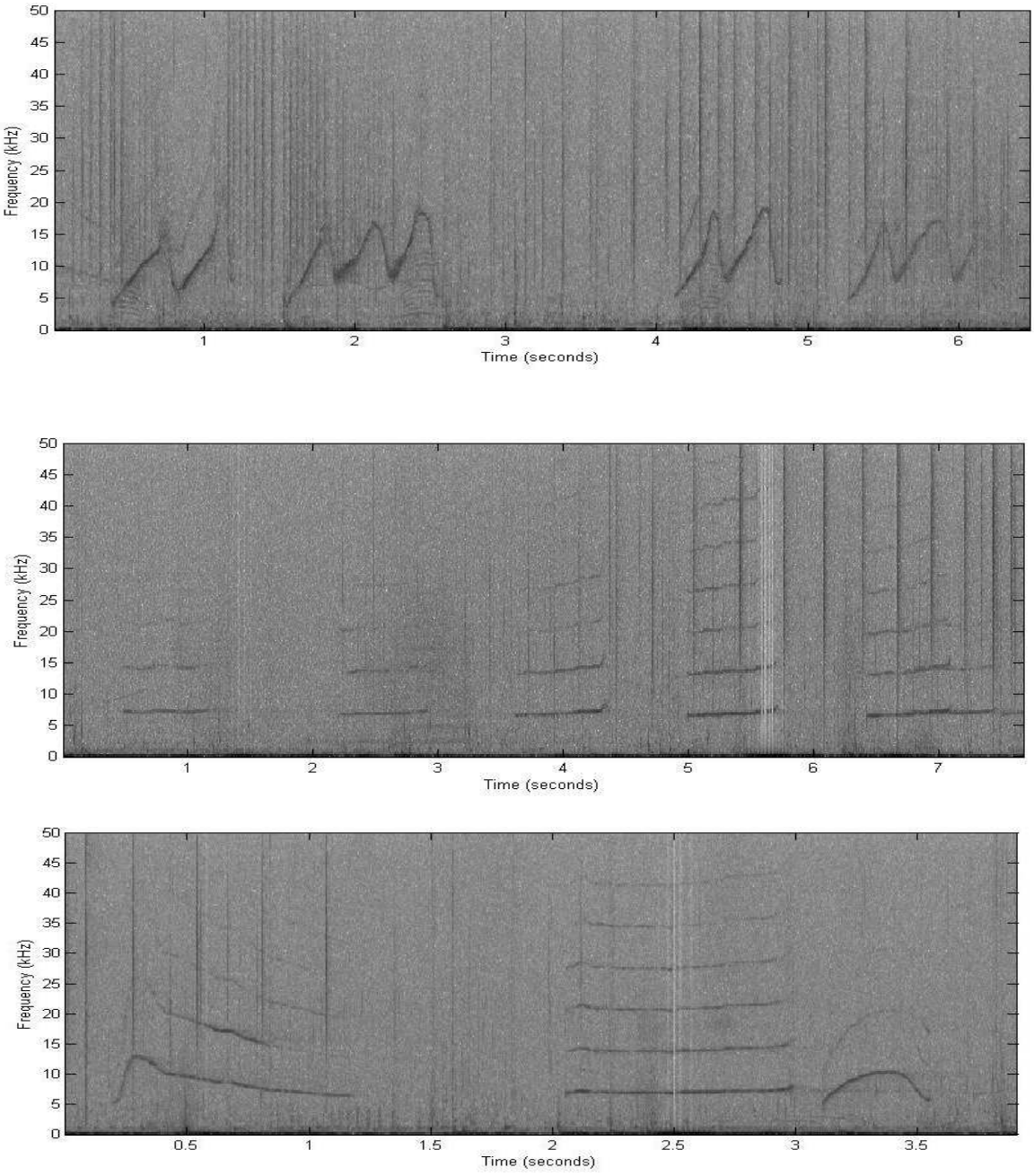

Figure 4.4c. No overlap, no match. Examples of no overlap, no match whistle sequences where non-overlapping whistles of the same or different type are produced in a sequence. The sampling rate is 100 kHz, FFT 2048, Hanning window function, and 100% overlap between FFT.

4.2.3 Randomisation Test

The times of both the brays and the three different whistle types (overlap match, overlap no match and no overlap, no match) were noted from the recordings. Only vocalisations with good signal to noise ratio were included in the analysis. To test whether overlap matching and bray calls occurred in close temporal proximity above chance levels a randomisation test was used. The time between the occurrence of a bray call and the occurrence of each of the three whistle types were noted. If one of the three whistle types occurred in a recording where brays were absent then the time from the whistle to the start or end of the recording (whichever was longest) was used.

The locations of the whistle types were then randomised 10000 times and their proximity to the nearest bray call re-calculated. The sampling static of interest was the mean time between each whistle type and the nearest bray call. The randomisation test was used to calculate the distributions of these proximities for each type under the null hypothesis that the locations of these whistle types were randomly distributed. The observed statistic was then compared to the random distribution.

4.3 Results

4.3.1 Initial Results

A total of 175 occurrences of the three whistle types occurred; 30 overlap matches, 55 overlap non-matches and 90 no overlap, no matches, see Table 4.2.

Table 4.2. The numbers of occurrences of the three whistle types, their mean proximity to bray calls and the mean number of whistles in one occurrence.

Whistle Type	# of occurrences	mean proximity to bray call (# of seconds)	mean # of whistles in one occurrence
overlap match	30	76 (range: 0.0001-627)	6 (range: 2-23)
overlap no match	55	399 (range: 0.0001-3138)	7 (range: 2 -47)
no overlap, no match	90	373 (range: 0.0001-3138)	4 (range: 2 -35)

The number of whistles of the same type that were overlapped for overlap matches was primarily two, indicating only two animals were participating in the matching event. There were instances of three animals involved in matching interactions (n=2), see Figure 4.5. Up to four different whistle types were found to be overlapping at any one time for overlap no match, indicating more than two animals were calling.

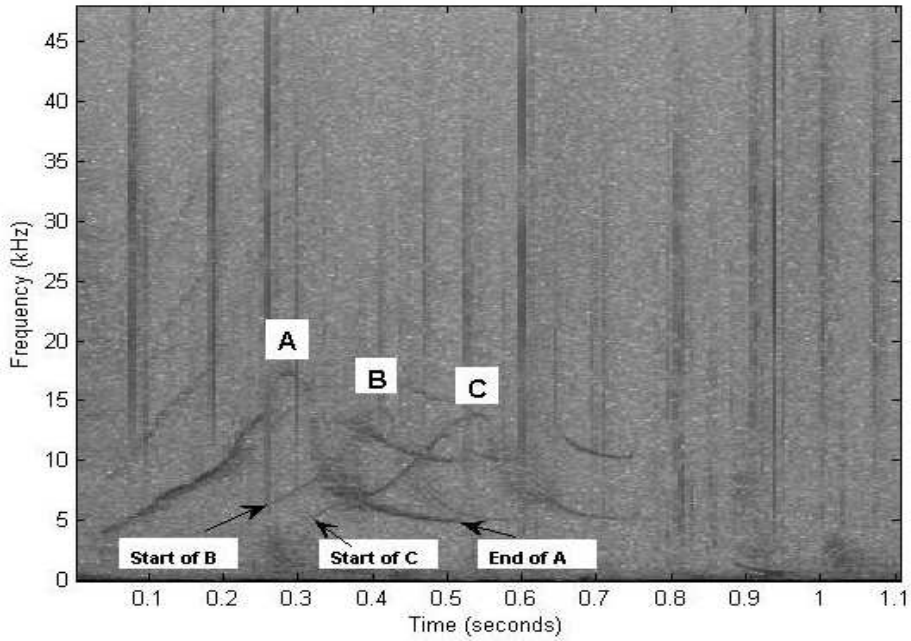

Figure 4.5. Example of three animals involved in an overlap match interaction, whistle B and whistle C both start before whistle A ends and overlap with one another.

Overlap matches always occurred in recordings where bray calls were present (Figure 4.6). Alternatively both overlap no matches and no overlap, no matches occurred in recordings where brays were both present and absent (Figure 4.6).

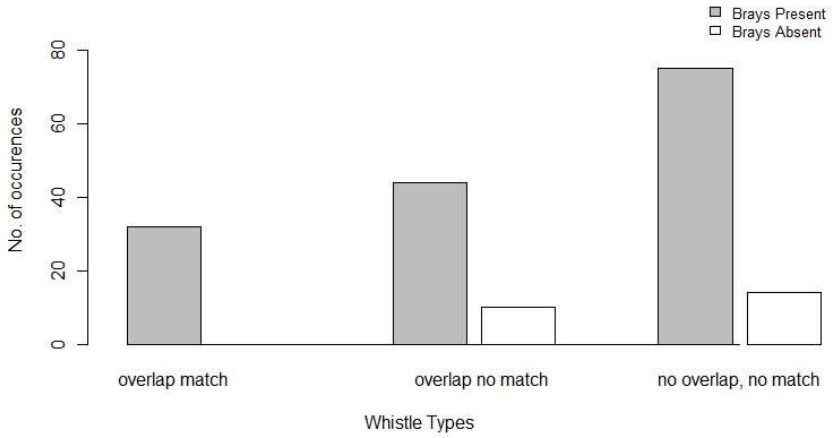

Figure 4.6. The number of occurrences of each whistle type in recordings where bray calls were present in recordings (black) and bray calls were absent from recordings (white).

4.3.2 Randomisation Test

Overlap matches and brays calls occurred in tight temporal proximity, with 75% of the occurrences of overlap matching occurring within 1 minute of a bray call. This observed value greatly exceeded the random distribution where only 55% occurred within 1 minute of a bray call and this difference was statistically significant (randomisation, $p < 0.0001$). This indicates that the rapid matching of call types appears to be closely synchronised with bray call production (Figure 4.7).

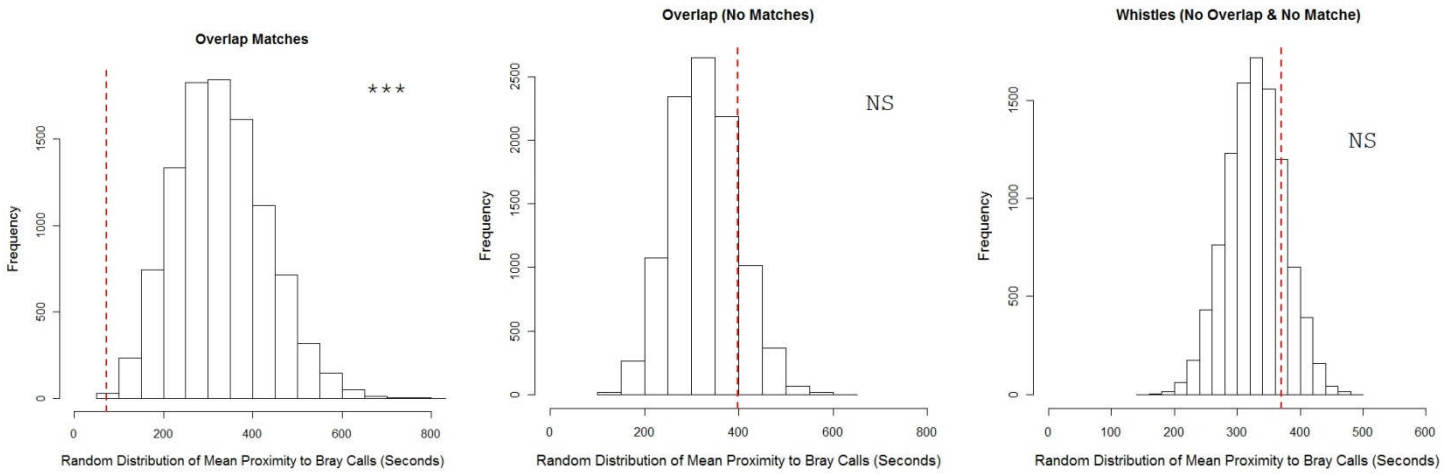

Figure 4.7. Histograms of the mean proximities, based on 10000 randomisations, of each whistle sequence type to the nearest bray call (seconds), the dotted line indicates the observed mean proximity.

Of the cases where whistles overlapped but did not match, only 48% occurred within 1 minute of a bray call and 39% were at least 5 minutes from the occurrence of a bray call. Finally for no overlap, no match, only 53% occurred within 1 minute and 30% at least 5 minutes from a bray call. Both overlap no match and no overlap, no match call production were no different to chance levels (Figure 4.7). Unfortunately I was not able to localise whistles to individuals and therefore I do not know whether no overlap matching occurred between multiple animals.

The difficulty of localising whistles to individuals means that the rates of matching may be much higher.

The timing of the overlap matches with respect to bray call production were compared to see if this vocal behaviour preceded braying bouts or followed them.

Figure 4.8. The location of overlap matches in relation to bray call production; they were produced before the onset of a braying bout, during, and after the end of a braying bout.

Many instances of overlap matching occurred simultaneously during a braying bout, yet equal numbers also occurred both before and after a braying bout (Figure 4.8).

4.4 Discussion

This analysis revealed that the rapid matching of whistle types correlates with foraging behaviour in the bottlenose dolphin. This is not a function of animals vocalising at random because the overlapping of different whistle types did not correlate with bray call production. This supports the notion that the rapid matching of same whistle types plays a specific role in the bottlenose dolphin communication system. These results are consistent with previous work (Janik 2000) and matching primarily occurred between two individuals. There were instances, however, where matching must have occurred between 3 animals (Figure 4.2a), although because I was unable to localise whistles to the individual it is possible that the number of animals matching at a given time could be higher.

These findings contrast with earlier work on dolphin species. Spinner dolphins (*Stenella longirostris*) forage cooperatively at night where they actively aggregate prey species (Benoit-Bird & Au, 2009). Whistles, however, were not detected during foraging behaviour, instead echolocation clicks were found to be produced (Benoit-Bird & Au, 2009). Another delphinid, the short-finned pilot whale (*Globicephala macrorhynchus*), is a deep diving social species that produces calls at depth (Jensen et al., 2011). Individuals forage during deep dives yet the lack of dive synchrony amongst these animals indicates that the production of these social calls does not seem to serve in cooperative foraging, but rather allows individuals within a social group to keep track of one another. Interestingly, in Sarasota Bay, Florida, single bottlenose dolphins produce whistles at higher rates when foraging alone in comparison to foraging in groups (Nowacek, 2005). Bottlenose dolphins, however, do not dive at extreme depths and the production of brays calls attracts conspecifics to the area (Janik 2000), and matching interactions in this population are most frequent in large group sizes (Janik 2000). The difference between the two studies is likely to be a reflection of foraging strategy. Animals may forage singly or in groups depending on type of prey species and the characteristics of the local environment. I have shown that this rapid

matching of call types is specific to foraging bouts where many animals are present, opening interesting avenues of thought to what the function may be.

4.4.1 Do bottlenose dolphins use whistle matching to locate specific individuals?

It may be that bottlenose dolphins match one another's signature whistles in order to address specific conspecifics. The matching of acoustic signals can function as a way of addressing particular individuals (Janik 2000; Tyack 2000; Todt 1981). We now know there seems to be a mechanism whereby vocal matching causes the matched animal to whistle in response (Chapter 3). By copying another dolphin's signature whistle, the copier may exchange information with specific individuals on their distance from one another. This exchange may be beneficial during foraging behaviours where animals socially manipulate prey behaviour. Yet the information in the call may be masked by high rates of call overlap and therefore other hypotheses must be considered.

4.4.2 Overlap matching: aggression versus affiliation

We know that vocal matching in some songbirds is known to have an aggressive function (Beecher et al., 2000; Searcy & Beecher, 2009). The overlapping of song types has been discussed as a threatening signal (Naguib & Mennill, 2010; Todt, 1981; Todt & Naguib, 2000), yet others disagree and state that overlapping does not occur above chance levels (Searcy & Beecher, 2009). Playback experiments with captive bottlenose dolphins have shown, however, that vocal matching, with signature whistles at least, does not induce aggressive states (Chapter 3). Alternatively overlap matching could also function as an affiliative signal by strengthening social bonds between individuals. This is true for male chimpanzees (*Pan troglodytes*) where two or more males produce temporally overlapping pant hoots (Mitani & Gros-Louis, 1998). During these exchanges males accommodate each other vocally, whereby pant hoots become more acoustically similar. Although not linked to foraging behaviour it is believed this serves to maintain and strengthen social bonds. The matching and overlapping of codas is also hypothesised to reinforce social bonds in sperm

whales (*Physeter macrocephalus*) (Schulz et al., 2008), primarily occurring during social periods and before and after long foraging dives. These interactions also occurred when animals were in visual contact, negating its use for localisation.

4.4.3 Does overlap matching function as an excitement call?

Another possibility is that the matching of acoustic signals may be the result of an emotive state or 'excitement calls'. Another dolphin species, the killer whale, produces an excitement call during high arousal behaviours, and this is found across ecotypes (Rehn et al., 2011). In the case of the bottlenose dolphin the production of a braying bout results in the fast approach of conspecifics to the area (Janik, 2000), although it is believed the function of bray calls is to exploit the perceptual system of the prey to facilitate capture. The fast approach of conspecifics and the larger group sizes found in this context may result in high arousal levels of animals due to social or feeding excitement. This high level of arousal may be the reason for the high rates of same whistle type overlap.

The chimpanzee is a species that forms fission-fusion societies, similar to the bottlenose dolphin. The chimpanzee produces a long-distance contact call, known as a pant-hoot, that is produced during chorusing bouts (Mitani & Gros-Louis, 1998). It was previously thought the high calling rate of pant-hoots between groups may be a result of high arousal levels due to social or feeding excitement. Instead individuals use pant-hoots to maintain spatial contact. The primary function of the pant-hoot, although indirectly informing conspecifics of the location of food, was the formation and maintenance of spatial separation between individuals (Mitani & Nishida, 1993). Thus rather than an excitement call, the overlap matching of call types in this study may result from animals calling to maintain spatial formation.

4.4.4 Does overlap matching regulate group movement?

The maintenance of group movement and spatial formation may be facilitated through vocal matching. For animals that live in close-knit groups the matching of call types functions in maintaining within-group contact as seen in killer whales (Miller et al., 2004); Japanese macaques (*Macaca fuscata*) (Sugiura, 1998); and greater horseshoe bats (*Rhinolophus ferrumequinum*) (Jones & Ransome, 1993). In addition many species use acoustic cues to coordinate group foraging, such as white-faced capuchins (Boinski, 1993) and green woodhoopoes (Radford 2004).

The matching of calls during foraging bouts may allow animals that are competing for food to regulate spacing. The pied-babbler uses a close call, called the 'chuck' to regulate spacing between foraging competitors (Radford & Ridley, 2008). Although not used aggressively, it did deter conspecifics that attempted to share an individual's foraging patch, and was effective in indicating the forager's current position. Pied-babblers increased chuck production rate when in larger groups, and when neighbours were closer (Radford & Ridley, 2008). Thus bottlenose dolphins may use the rapid matching of call types to regulate the spacing of individuals during intensive feeding bouts where group sizes are large.

4.4.5 Conclusion

To summarise, I have shown that the overlap matching of whistles is tightly correlated to bray call production and thus plays a role in foraging in the bottlenose dolphin.

We know that high rates of whistle overlap may hinder caller localisation, but we also know that whistle matching can occur without the overlapping of the whistles (Janik, 2000). It may be that vocal matching is multifaceted and bottlenose dolphins may vary the timing between vocal matches in order to indicate their level of intention or motivational state. The rapid matching (overlapping) of call types may signal an affiliative or excited state and assist

in regulating spatial formation of groups during foraging. At the same time, slightly delayed vocal matching with little overlap may facilitate the localisation of specific individuals, allowing animals to address one another (Bremond, 1968; Todt, 1981; Janik, 2000; Chapter 3). It is conceivable that vocal matching has an interchangeable function that is dependent on both the context and the motivation and intention of the respondent, and that this information is encoded in the temporal sequencing of the vocal match.

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Chapter 5

Vocal Imitation of Individual Signature Whistles in Bottlenose Dolphins (*Tursiops truncatus*)

5.1 Introduction

Vocal production learning enables animals to copy novel sounds in their environment and develop their own individually distinctive repertoire of calls (Janik and Slater 1997). The use of vocal learning is particularly widespread in two contexts. In songbirds (Catchpole and Slater 2008), phocid seals (Janik and Slater 1997) and baleen whales (Janik 2009a) vocal learning is important in intra- and inter-sexual selection because it shapes male song. In delphinids (Janik 2009b) and elephants (Poole et al., 2005) learning appears to primarily help in the development of individual- or group-specific calls or repertoires used for individual or group recognition. Bats seem to use vocal learning in both of these contexts (Boughman 1998; Knornschild et al., 2010). In those species where vocal learning allows the development of individually-distinctive calls, this vocal plasticity may be used to address conspecifics. The addressing of individuals may play a role in social affiliation but could also be used in aggression or deception.

Bottlenose dolphins produce individually distinctive signature whistles (Caldwell & Caldwell 1965; Sayigh et al., 2007; Caldwell et al., 1990) that develop under the influence of vocal learning (Fripp et al., 2005; Miksis et al., 2002; Tyack and Sayigh 1997). They are one of the very few species that learn novel signals that are unique to each animal. Copying of these individually distinctive signature whistles for addressing would be a lot less equivocal than

addressing in other animals, making bottlenose dolphins a particularly interesting case for the study of functional aspects of copying skills.

The signature whistle is the most common and often the only whistle type used by isolated captive dolphins, which makes these whistles easy to identify (Caldwell et al., 1990). Signature whistle use in wild, free-ranging animals constitutes 38% to 70% of their whistle vocalisations, depending on the social context (Buckstaff 2004; Cook et al., 2004; Watwood et al., 2005). Signature whistles contain identity information that is encoded in the unique frequency modulation pattern, developed by each individual early in life (Janik et al., 2006). They function in both individual recognition and in maintaining group cohesion (Janik and Slater 1998; Sayigh et al., 1999). While the signature whistle is a very stable component of an individual's vocal repertoire (Sayigh et al., 1990), bottlenose dolphins can also substantially modify their vocalizations through vocal learning, an ability they maintain throughout their adult life (Richards et al., 1984). Their capability for vocal learning means that one animal's signature whistle can be copied by other individuals (Tyack and Sayigh 1997; Janik and Slater 1998; Tyack 1986; Tyack 1991). However, with the exception of one pair of animals in which it appears that high copying rates have been induced by the methods used (Tyack 1986; Tyack 1991), copying events are rare (Watwood et al., 2005; Janik and Slater 1998; Janik 2000) albeit significantly more common than expected by chance (Janik 2000). Thus, a particular signature whistle type might be found in the repertoire of more than one individual, but there is a paramount difference in the frequency with which it is used by different dolphins, making it a reliable indicator of identity of the main user or owner of the whistle, despite occasional copying events.

Despite this substantial work on bottlenose dolphin signature whistles, the function of copying events remains relatively unclear. Unlike songbirds, delphinids are not territorial and do not sing. Instead they use their acoustic signals in the context of social interactions and group

cohesion (Janik 2009b). One hypothesis is that, in contrast to song matching in birds, the copying of signature whistle types is used in an affiliative way. It may be a method of initiating contact with an individual (Tyack 1991), either spontaneously or in response through vocal matching. Janik (2000), however, reported overlapping whistle matching between up to three individuals in the wild, suggesting that matching may also be used in other contexts. A second hypothesis is that matching is used as a signal of aggressive intent, similar to some songbirds (Todt & Naguib 2000). A third hypothesis is that whistle copying is used as a deceptive form of signalling (Janik 1999a). It appears that copies are sufficiently rare to allow for such a use without jeopardizing the reliability of signature whistles as identity signals.

To investigate these three hypotheses, the occurrence of signature whistle copying was studied in a temporary capture-release context, in which animals were physically restrained and could not reunite at will. It was hypothesised that if signature whistle copying is affiliative it should only occur between close associates. Copying in an aggressive context should be more common between animals that were less closely associated. Furthermore, copies used in a deceptive way should ideally not be recognizable as copies, while in other contexts they can be. Thus, by identifying who copied who, and how well, the underlying function of the copying of individually specific identity signals in a non-human communication system that may use learned signals in a functionally referential way may begin to be uncovered.

5.2 Material and Methods

5.2.1 Social and acoustic data from the wild

The amount of time animals are sighted together can be used to give a measure of their association, e.g. the half-weight ratio coefficients of association (CoA) (Ginsberg & Young 1992). These were calculated for all the study animals from data gained during photo identification surveys of dolphins in the year before each capture event. CoAs given for each pair are the CoAs from the year before recordings were taken. Wild bottlenose dolphin acoustic recordings were collected during capture-release events for health assessments and life history studies in Sarasota Bay, Florida, USA between 1984 and 2009 (Wells et al., 2004). One such event takes on average 108 min from the time the net is set to the time the individual is returned to the water from the veterinary examination vessel. During these events, animals were physically restrained and frequently out of visual sight, but not acoustic range, of one another. Ages of animals were known from long-term observations (R.S. Wells 2003) or from analyzing growth rings in extracted teeth (Hohn et al., 1989). The signature whistle of an individual was defined by (Caldwell et al., 1990) as the most common whistle type emitted in such isolation conditions. Using this approach the Sarasota Dolphin Research Program has accumulated a catalog of whistles from over 200 individual dolphins from the long-term resident community in Sarasota Bay since 1975 (Sayigh et al., 2007), many of which were recorded on multiple occasions. In this study all whistles produced by an individual were compared to the signature whistles in the catalog in order to identify copying events.

The vocalizations of each individual were recorded via a suction cup hydrophone, allowing the identification of the caller for each recorded call. Either custom-built or High Tech Inc. SSQ94 hydrophones were used. Between 1984 and 2004 the acoustic recordings were taken

with either Marantz PMD-430 or Sony TC-D5M stereo-cassette recorders (frequency response: 20–18000 Hz ± 5 dB) or Panasonic AG-6400 or AG-7400 video-cassette recorders (frequency response flat from 20–32000 Hz). For recordings taken from 2005 onwards a Sound Devices 744T digital recorder (frequency response: 10-48000 Hz ± 1 dB) was used.

The first step of analysis involved scanning by eye spectrograms of 205 hours and 23 minutes of acoustic recordings of temporarily caught and released wild bottlenose dolphins in order to identify copying events. The CoA is a measure of the frequency with which two animals associate with one another with values ranging from 0.00 (never sighted together) to 1.00 (always sighted together) (Owen et al., 2002). The minimum CoA for a closely bonded animal, such as a male pair, is 0.5 (Owen et al., 2002; Watwood et al., 2004) The total recording time analysed was 110 hours and 55 minutes for pairs of animals with low association levels (CoA<0.5) and 94 hours and 28 minutes for pairs with high association levels (CoA>0.5). The second step involved a more detailed analysis of 32 hours and 12 minutes (Table 5.1) of recordings where vocal copying had been found.

In total 85 different capture-release events of wild dolphins were analysed, comprising 121 individuals in different group compositions. Of these, 48 were sampled on more than one occasion (range: 2-7). Of the 85 capture-release events analysed, 11 consisted of single male-male pairs, 31 of single mother-calf pairs and the remaining 43 consisted of groups of different compositions. These compositions included 2 or more adults of the same or both sexes, mother-calf pairs with other adults, and groups of mother-calf pairs.

5.2.2 Social and acoustic data from captivity

To investigate the social context of copying, four captive adult males were recorded at The Seas Aquarium, Orlando, USA, during May-June 2009. One male, Ranier, was estimated to be 28 years old and was caught at approximately three years of age in the Gulf of Mexico. The other males were Calvin (15 years old), Khyber (18 years old), and Malabar (8 years old), who were all captive born. All four animals had been together for 3.5 years at the start of the study; Ranier and Calvin had been together for 6 years. Vocalizations of captive dolphins were recorded with two HTI-96 MIN hydrophones (frequency response: 0.002 to 30 kHz ±1 dB) and two CRT hydrophones (C54 series; frequency response: 0.016 to 44 kHz ±3 dB) onto a Toshiba Satellite Pro Laptop using a 4 channel Avisoft 416 UltrasoundGate recording device (sampled at 50 kHz, 8 bit).

A total recording time of 16 hours for the 4 males was analysed. The percentage of time where the copying between pairs could be identified (as determined by their positions in the pool system) was as follows; 100% for Ranier and Calvin, Ranier and Malabar, Khyber and Calvin and Khyber and Malabar; 87.3% for Ranier and Khyber and 12.7% for Calvin and Malabar. The caller was identified using passive acoustic localisation. The social association of male pairs at The Seas was evaluated by measuring synchrony in their swimming patterns (Connor et al., 2006). A focal animal, instantaneous sampling method, was used with an observation period of 7.5 minutes and a 15-second interval. At each 15-second interval, the focal animal's synchrony status was assessed relative to each other animal in the group. Observations took place five days per week between 0800 and 1800, and each animal served as the focal animal once each day in an order determined by a balanced, randomly-ordered schedule. Observations made between Jan 2009 and June 2009 were analysed in which all four dolphins were together in the same group (data collected by W. Fellner from The Seas).

5.2.3 Identifying copying events

Initially, I identified all occurrences where the same whistle type was being produced by more than one animal within a recording session, by inspecting spectrograms (FFT length 512, overlap 100%, Blackmann-Harris window) in Adobe Audition v2.0 (Adobe Systems). Five naïve human observers were then used to rate the similarity of each vocal copy of a signature whistle to the original signature whistle (the whistle as produced by its owner) and to the copier's own signature whistle. Visual classification is more reliable than computer-based methods in dolphin whistle classification (Sayigh et al., 2007; Janik 1999b) and is frequently used in animal communication studies (Catchpole & Slater 2008; Garland et al., 2011). The five observers were blind to context and animal identity. They were given the extracted contours (frequency modulation pattern) of the whistles as plots of frequency versus time and were asked to rate whistle similarity using a 5 point similarity index ranging from 1(dissimilar) to 5 (similar). Only copied whistles that reached a mean similarity score of > 3 with the original signature whistle and < 3 with the copier's own signature whistle were deemed vocal copies and included in the analyses. A value of 3 indicates a relatively high similarity as indicated in previous studies (Janik 2000; Watwood et al., 2004)

5.2.4 Acoustic analysis

The whistle contours of every vocal copy as well as of randomly chosen exemplars of signature whistles of both interacting individuals were extracted using a supervised contour extraction program (Deecke & Janik 2006). Contours had a time resolution of 5 ms. The following parameters were measured from the contours: start frequency, end frequency, minimum frequency, maximum frequency, frequency range, duration, and mean frequency. One further

parameter, number of loops, was read directly from the spectrogram where applicable. A loop was defined as a repeated modulation pattern within a signature whistle that could be separated by periods of stereotyped, discrete segments of silence (Caldwell et al. 1990). These periods of silence were taken to be 250ms or less, which is the maximum inter-loop interval found in this population (Esch, Sayigh & Wells 2009).

5.2.5 Statistical Analysis

All statistical procedures were conducted in R (R project for statistical computing; GNU project). Acoustic parameters were analysed by first testing for normality using the Lilliefors (Kolmogorov-Smirnov) test. Depending upon the outcome, either the Mann-Whitney test or a Welch's t test was used to compare differences between parameters of the copies with the original signature whistles and the copier's own signature whistle. A sampling statistic was then created that was the combined test statistic for all parameters, calculated by multiplying the test statistics for each parameter test together. This allowed comparisons of overall difference between two whistle types. A permutation test was used to shuffle the acoustic parameter measurements of the vocal copies with those of the original signature whistles within each pair of animals. This was done to test whether the combined acoustic parameter statistic was significantly different from a random distribution. The permutation test performed 10000 permutations to calculate the distribution of the test statistic under the null hypothesis (random distribution), and the observed test statistic was then compared to this random distribution. A two-tailed test was used with a Bonferroni--adjusted significance level of $p < 0.002$. In addition, all parameters were used in a non-metric multi-dimensional scaling analysis with a good STRESS fit of 0.04.

A permutation test was also used to test whether signal copying only occurred between affiliated pairs of animals. This involved shuffling the CoAs of the pairs of animals who produced

vocal copies (n=11) with those that did not (n=191). Many of the individuals who copied were also in pairs with other animals where copying was not present. The sampling statistic of interest was the mean CoA for the pairs involved in signal copying. The permutation test performed 10000 permutations to calculate the distribution of the test statistic under the null hypothesis that the CoAs of copiers were randomly distributed. The observed test statistic was then compared to the random distribution. Permutation tests were also performed on the timing of the copies after the original signature whistle. The times of the copies (n=108) were shuffled with the times of the copier's own signature whistles (n=1651) after the original signature whistle. The random distribution was calculated from 10000 permutations under the null hypothesis that there was no difference between the timing of copies of signature whistles after the occurrence of the template whistle and the timing of the copier's own signature whistle after the occurrence of the template whistle. The observed test statistic (mean time between original signature whistle and the copy) was compared to the random distribution.

5.3 Results

5.3.1 Who copies who?

As in previous studies (Sayigh et al., 2007; Sayigh et al., 1990), each bottlenose dolphin almost exclusively used its own, individually distinctive signature whistle during capture-release events. Whistle rates are generally high at these events with a mean of 10.9 whistles/min/individual (Esch et al., 2009). However, in 10 out of 85 different capture-release sets, individuals were found occasionally copying the signature whistle of another animal in the set (mean rate 0.18 copies/min/individual). This occurred in 10 out of 179 pairs of animals recorded from 1988 through 2004, consisting of 2 of the 11 male-male pairings and 8 of the 31 mother-calf pairs. In some instances both members of a pair copied one another (Figure 5.1, Table 5.1, Appendix 1). The total number of individuals who produced vocal copies was therefore 12. Human judges viewed frequency contour plots of whistles to quantify similarity of the copies with both the originals and the copier's own signature whistles on a 5-point scale and showed statistically significant agreement (Kappa = 0.42, $z = 29.9$, $P < 0.0001$ (Siegel & Castellan 1988)). Similarity values for all copies are given in Table 5.1.

Table 5.1. Pairs of animals involved in signature whistle copying events, with the animal producing copies in bold. The mean similarity values are given for each animal's signature whistle when compared to the vocal copy. The copier's own signature whistle (in bold) has a low similarity score with the copy while the signature whistles of the copied animals have high similarity scores with the copy (see Appendix 1).

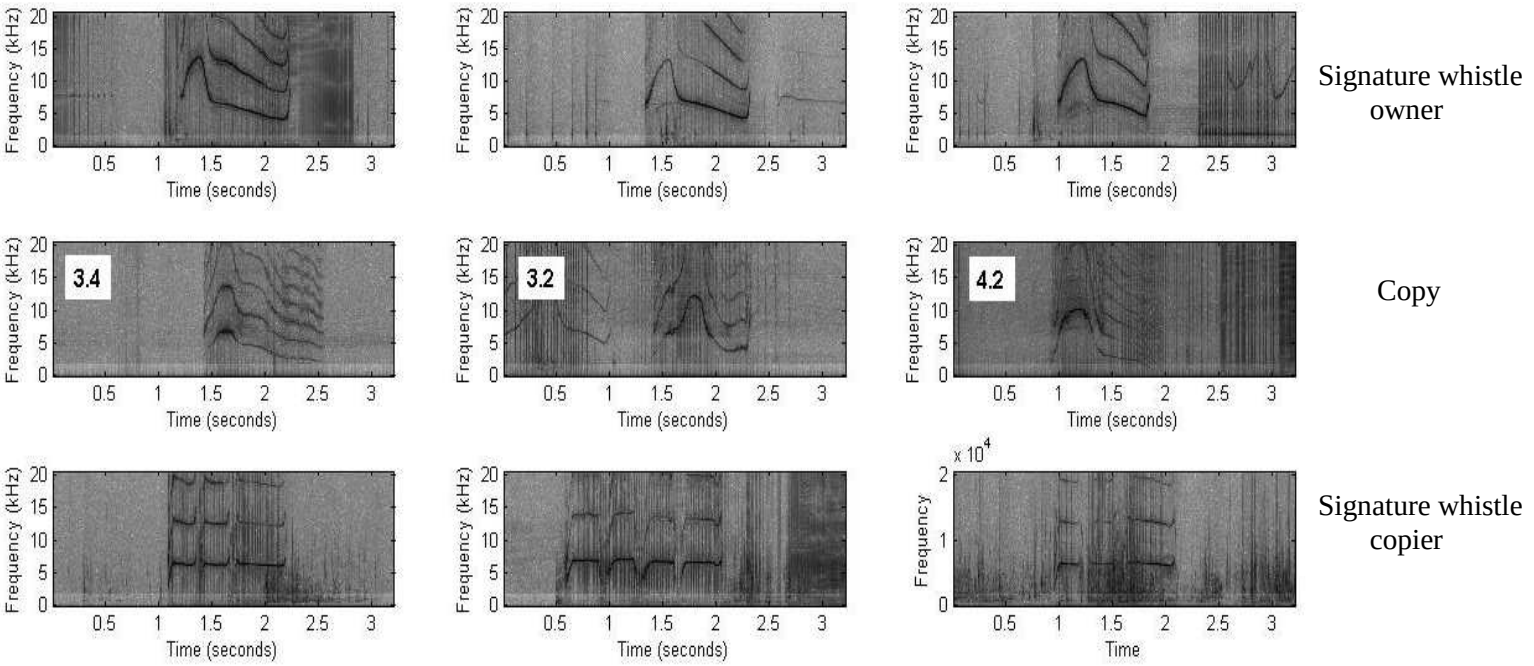
Pair	Year of Recording	Sex	Relationship	COA	Age	No. of animals in the session	Recording Time (minutes)	No. of Vocal Copies	Average Similarity Values
1. Calvin	2009	M	Associates	1*	15	4	70	13	1.5
Ranier		M			28		70	-	4.5
2a. FB26	1988/2000	M	Alliances	0.8	31	2/4	93	38	1.0 / 3.2 §
2b. FB48		M	Partners		29		101	5	1.0 / 3.5 §
3. FB114	2004	M	Associates	0.07	16	2	51	4	2.4
FB20		M			15		95	-	3.3
4. FB90	1995	F	Mother	0.98	25	2	92	17	1.3
FB122		M	Calf		4		92	-	3.3
5. FB65	1989	F	Calf	0.67	6	2	70	1	1.2
FB67		F	Mother		21		70	-	3.6
6. FB228	2004	M	Calf	0.95	5	2	106	8	1.1
FB65		F	Mother		21		106	-	3.5
7. FB5	1989	F	Mother	1.0	29	4	85	17	1.3
FB55		F	Calf		3		85	-	3.3
8a. FB35	1988	F	Mother	0.9	32	3	92	2	1.7 / 3.7 §
8b. FB93		F	Calf		3		92	4	2.5 / 3.2 §
9. FB71	1989	F	Mother	1.0	28	2	97	13	1.0
FB95		F	Calf		1		97	-	3.3
10. FB5	1992	F	Mother	0.56	29	2	79	40	1.0
FB155		F	Calf		2		79	-	3.5
11. FB9	2004	F	Mother	0.9	20	2	105	9	1.2
FB177		F	Calf			2	105	-	3.4

* These animals were permanent residents in a captive facility.

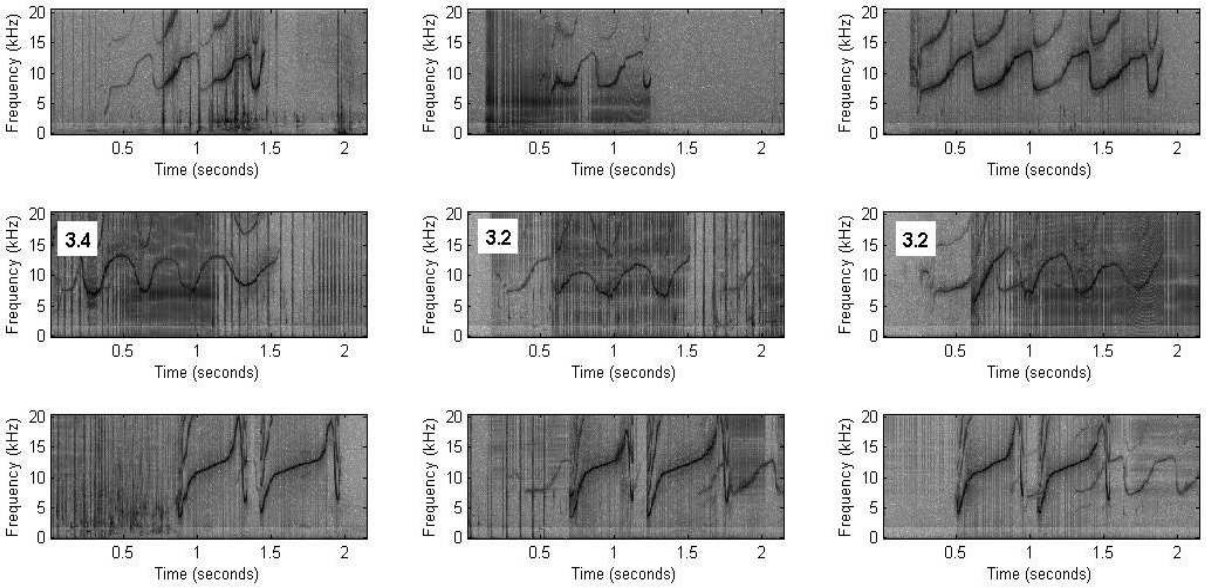
§ Where both animals copied one another the average similarity value for that animal's own signature with the copy it produced of the other animal's signature whistle is given first (low number) followed by the average similarity value for that animal's own signature whistle with the copy produced by the other animal in the pair (larger number)

Figure 5.1 - Signature whistle copies
Spectrograms showing three examples each of the signature whistle of the animal being copied (top line), signature whistle copies (middle line) and the signature whistle of the copier (bottom line); sampling rate is 40000 Hz, FFT length 1024, Hanning window function. Numbers on the middle spectrograms give the mean human observer similarity scores between the original and the copy for each pair of whistles on a scale from 1 (not similar) to 5 (very similar).

A. The interacting animals were a mother-calf pair; the mother, FB65, was the signature whistle owner (top) and the male calf, FB228, was the copier (bottom), the copies he produced are in the middle.



B. The interacting animals were a mother-calf pair; the male calf, FB122, was the signature whistle owner (top) and the mother, FB90, was the copier (bottom), the copies she produced are in the middle.

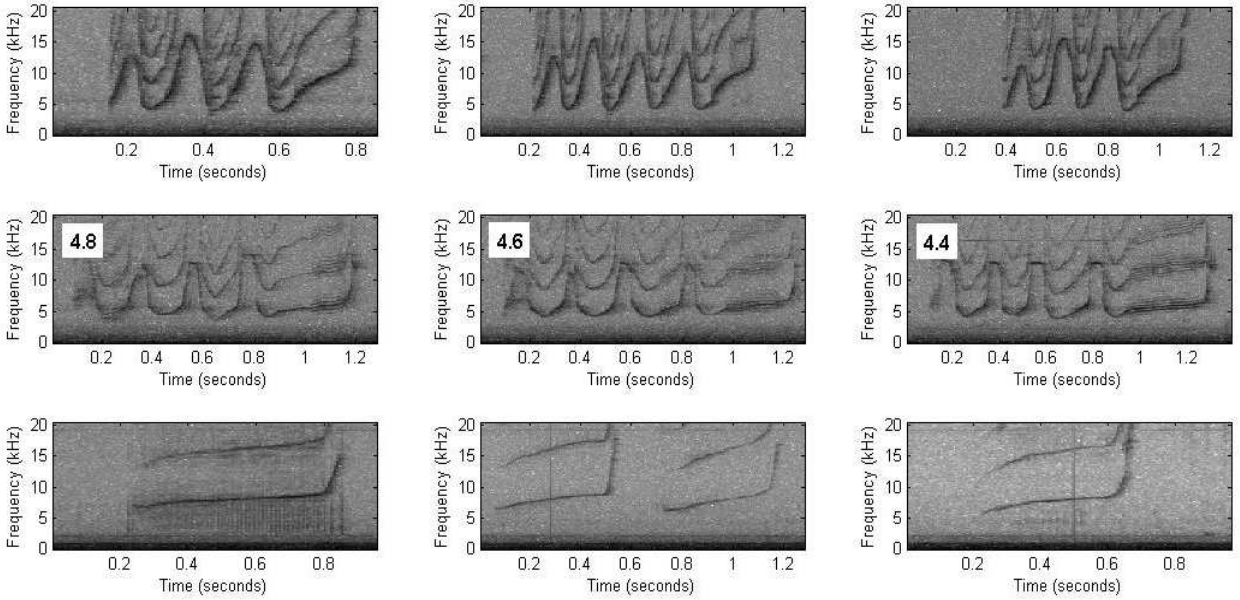


Signature whistle owner

Copy

Signature whistle copier

C. The interacting animals were a male-male pair; an adult male, Ranier, was the signature whistle owner (top) and the second adult male, Calvin, was the copier (bottom), the copies he produced are in the middle.



Signature whistle owner

Copy

Signature whistle copier

The results of a permutation test clearly show that signature whistle copying occurred between closely affiliated pairs of animals ($p=0.0006$). The mean half-weight coefficient of association (CoA; which can range from 0 to 1) (Ginsberg & Young 1992) for the 10 pairs of animals was 0.8, while the mean CoA for non-copiers was 0.4 (Figure 5.2).

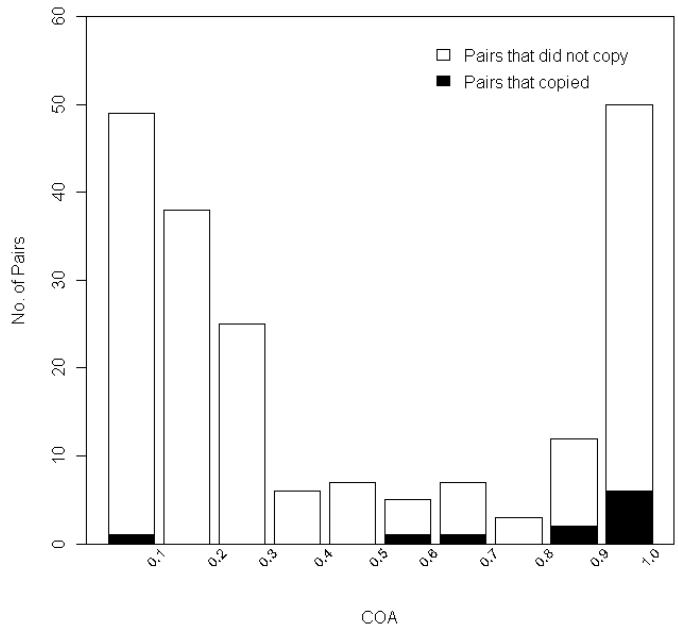


Figure 5.2. Coefficients of association (CoAs). CoAs of the pairs of animals that copied (black) and did not copy (white). The y axis is the number of pairs of animals (n=202) and the CoA in the year prior to the recording is on the x-axis.

In recordings of four captive males (forming six possible pairs) at The Seas, one pair also engaged in signature whistle copying. These two individuals showed high levels of synchronous behaviour (23% of 285 min of observation time) in the pool. Synchrony is a sign of social bonding in male bottlenose dolphins (Connor et al. 2006). One exchange of signature whistle copying between these males was 30 seconds in duration: both males emitted the signature whistle of one of them in an interactive sequence consisting of 13 and 11 renditions respectively (Figure 5.3). Copying in these individuals was not accompanied by aggressive behaviour (total observation time 16 hours with 13 copies produced). The synchrony of the other male pairs was

generally lower (7-13% of the observation time). One other pair, however, had a high level of synchrony (26%) but did not engage in whistle copying in 16 hours of recording. Thus, copying is not necessarily common in bonded males.

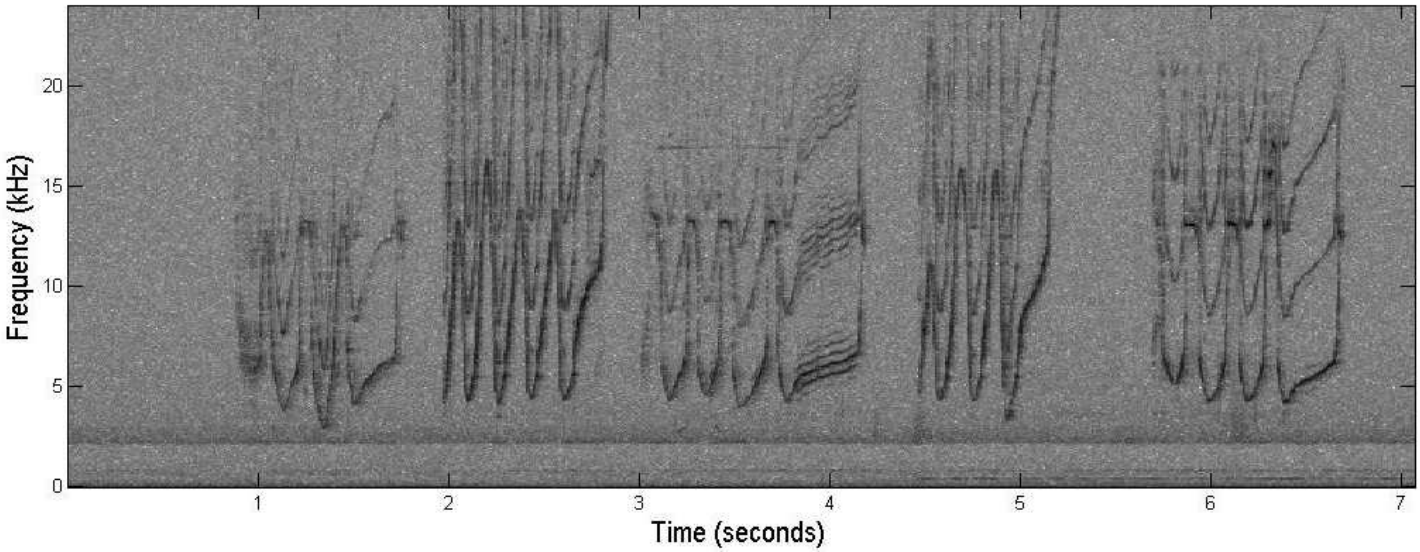
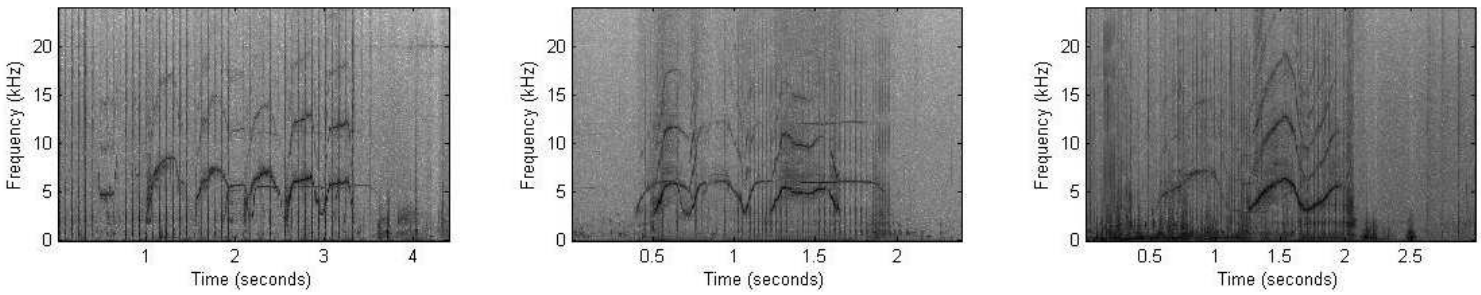


Figure 5.3. Section of a signature whistle copying sequence that occurred between two captive adult male bottlenose dolphins (Calvin and Ranier): sampling rate is 48000 Hz, FFT length 1024, Hanning window function. This section begins with Calvin's copy of Ranier followed by an alternation between the two males i.e. Calvin copy of Ranier, Ranier signature whistle, Calvin copies, Ranier signature whistle, Calvin copies (see figure 5.1 for signature whistles of Calvin).

Interestingly there were also 3 instances of overlapping non-signature whistle copying between 2 adult, wild females of low association (Figure 5.4a). These animals also produced their own signature whistles but no signature whistle copies.

A.



B.

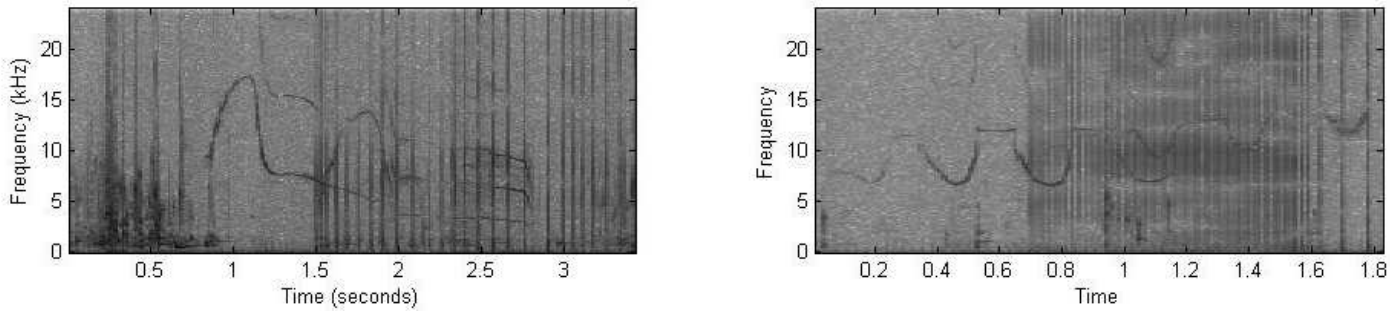


Figure 5.4. A. Examples of non-signature whistle matching that occurred between two adult females, FB33 and FB8: sampling rate is 48 kHz, FFT length 256, Hanning window function. The animals had a CoA of 0.1 for the year prior to recording. **B.** Examples of signature whistle copies that overlapped with the signature whistle emitted by the owner: sampling rate is 48 kHz, FFT length 256, Hanning window function. Left: calf FB228 copying his mother FB65 (top whistle); right: adult male FB114 copying another adult male, FB20 (bottom whistle), who was a close associate at the time of recording.

5.3.2 How accurate are vocal copies?

Frequency parameter measurements of copies produced by 11 animals (one captive and 10 wild animals; two wild copiers were excluded due to small sample sizes) revealed consistent differences between signature whistle copies and the original, copied signature whistle (Table 5.2, Figure 5.4). While the overall frequency modulation pattern of the copied whistle showed high similarity to the original (Figure 5.1), copiers introduced consistent variation in single acoustic parameters such as the start or end frequency (Table 5.3). In these parameters, copies were often closer to other whistle contours than to the copied signature whistle (Figure 5.5).

Table 5.2. Test statistics for all acoustic parameter measurements combined for each copy and original signature whistle comparison. Shown are the sampling statistic of actual combined parameter measurements (observed), and the mean test statistic of combined parameter measurements under the null hypothesis based on 10 000 permutations (expected). Differences between acoustic parameter measurements of vocal copies and original signature whistles are significant at a level of $p < 0.002$.

	observed test statistic	expected test statistic	p
Ranier vs. copy of Ranier	- 7.52	-0.002	0.002
FB48 vs. copy of FB48	0.19	- 0.007	0.12
FB26 vs. copy of FB26	559	0.025	< 0.0001
FB20 vs. copy of FB20	166	0.43	0.0031
FB122 vs. copy of FB122	0.27	0.003	0.1
FB65 vs. copy of FB65	1004	0.03	< 0.0001
FB55 vs. copy of FB55	24000	0.016	< 0.0001
FB35 vs. copy of FB35	125	- 0.01	< 0.0001
FB95 vs. copy of FB95	- 1439	- 0.01	< 0.0001
FB155 vs. copy of FB155	3071589	1.85	< 0.0001
FB177 vs. copy of FB177	-2646	-0.0003	< 0.0001

Table 5.3

Mean ± SD for frequency parameter measurements from each signature whistle copy (bold) compared with the original signature whistle and the copier's own signature whistle. Statistical comparisons were made either with Mann-Whitney test for non-parametric data or Welch's t test

* indicates significant differences (· p<0.05; *p<0.01; **p<0.001; ***p<0.0001). Note that tests of parameters on the same whistle might not be independent and therefore could have an effect on the test provided here. This is not, however, a problem for the permutation tests (Table 5.2).

	N	Start Freq. (kHz)	End Freq. (kHz)	Minimum Freq. (kHz)	Maximum Freq. (kHz)	Frequency Range (kHz)	Duration (seconds)	Mean Freq. (kHz)
		Mean ± SD	*Mean ± SD*	*Mean ± SD*	*Mean ± SD*	*Mean ± SD*	*Mean ± SD*	*Mean ± SD*
FB65	10	**8.0±0.6***	**8.5±1.2***	**4.7±0.1***	**14.6 ±0.4*****	9.8±0.5	**0.8±0.08** ·	**8.1±0.4***
copy of FB65	8	4.4± 2.1	4.2±3.9	2.5±2.2	11.6±1.9	9.1±2.6	1.0±0.2	6.0±1.7
FB228	12	4.1±1.2	6.3±1.2	3.6±0.9	**8.7±2.9** ·	**5.1±3.4****	1.0±0.4	6.8±0.6
FB155	11	5.7±1.2	**3.5±0.1*****	**3.5±0.1*****	**12.7±0.4*****	**9.2±0.4 ***	**0.95±0.14*****	**7.6±0.2*****
copy of FB155	40	6.1±0.6	7.3±1.1	5.6±0.6	14.0±2	8.3±2	0.86±0.07	10.8±1.1
FB5	10	**5.4±0.7 ***	**24.6±3.2*****	**5.1±0.8** ·	**24.6±3.2*****	**19.5±3.5*****	**0.75±0.05*****	**12.3±0.7*****
FB177	14	7.1±0.8	**9.8±1.4*****	6.7±0.8	**17.3±0.7*****	**10.6±1.1*****	**0.79±0.4***	**12.3±0.7*****
copy of FB177	9	7.2±0.6	7.7±0.8	6.8±0.5	11.5±1.3	4.6±1.2	0.4±0.05	9.4±0.5
FB9	11	7.5±0.7	**14.4±1.7*****	6.6±0.2	**14.6±1.9*****	**8.0±1.8*****	**0.59±0.25** ·	9.4±0.4
FB55	15	**5.8±1.4** ·	**5.3±0.5*****	**4.9±0.3*****	**12.5±0.5*****	**7.6±0.7*****	0.67±0.4	**8.0±0.4*****
copy of FB55	17	6.3±1.3	9.0±1.9	6.0±0.8	18.5±2.0	12.5±1.8	0.7±0.19	12.5±1.3
FB5	10	5.7±0.6	**26.8±4.9*****	5.6±0.5	**26.8±4.9*****	**21.1±5.2*****	0.76±0.08	12.7±1.0

	N	Start Freq. (kHz)	End Freq. (kHz)	Minimum Freq. (kHz)	Maximum Freq. (kHz)	Frequency Range (kHz)	Duration (seconds)	Mean Freq. (kHz)
		Mean ± SD	*Mean ± SD*	*Mean ± SD*	*Mean ± SD*	*Mean ± SD*	*Mean ± SD*	*Mean ± SD*
FB122	10	9.3±3.1	13.0±1.5	**4.5±1.0***	**14.4±0.2***	9.8±1.0	1.0±0.3	**10.5±0.2** ·
copy of FB122	17	7.9±3.7	12.8±2.6	6.1±1.3	15.9±2.3	9.8±2.5	1.0±0.4	11.3±1.2
FB90	10	6.5±0.6	11.2±1.9	**4.3±0.6*****	**21.6±1.2*****	**17.2±1.6*****	0.77±0.29	12.0±0.6
FB35	5	**13.3±0.5*****	**17.7±1.5 ***	5.7±0.4	**17.7±1.5***	**11.9±1.5***	1.0±0.1	8.8±0.5
copy of FB35	4	11.6±0.4	14.5±1.0	6.0±0.5	14.6±1.0	8.6±1.0	1.1±0.06	9.6±0.5
FB93	9	10.9±1.0	**8.7±2.2*****	**4.8±0.6***	14.3±0.8	9.5±1.0	**0.8±0.1*****	9.5±0.5
FB20	6	6.3±1.1	6.9±3.2	5.4±0.4	**11.5±0.9 ***	6.1±0.9	1.2±0.2	**8.3±0.3***
copy of FB20	4	9.8±4.7	12.4±4.1	8.1±3.4	14.5±1.5	6.4±2.3	1.1±0.1	11.4±2.7
FB114	5	5.8±1.4	7.1±4.9	4.7±1.3	12.8±1.6	8.1±2.2	**1.4±0.2***	8.3±0.4
FB95	10	8.9±0.3	20.1±2.3	**8.7±0.3*****	**20±2.2***	**11.5±2.1****	**0.8±0.1***	**12.3±0.1*****
copy of FB95	13	8.3±1.6	22.3±3.1	6.8±1.2	22.8±2.5	15.9±3.3	0.6±0.1	13.8±1.2
FB71	10	**6.7±0.2***	22.6±3.7	6.1±0.8	23.5±3.1	17.4±3.3	**1.1±0.4***	**12.8±0.9** ·
FB48	17	6.2±1.3	6.5±0.8	4.6±0.8	14.1±0.2	9.5±0.9	0.9±0.2	**9.3±0.2*****
copy of FB48	38	5.8±2.0	6.6±1.7	5.0±1.1	14±0.2	9.0±1.1	0.8±0.1	9.9±0.3
FB26	5	5.6±1.7	**4.5±0.3*****	**4.1±0.4***·	14.1±0.1	**9.9±0.4 ***	0.85±0.1	**8.5±0.3*****
FB26	5	5.6±1.7	**4.5±0.3****	**4.1±0.4***	**14.1±0.1*****	**9.9±0.4*****	0.85±0.1	**8.5±0.3*****
copy of FB26	5	6.1±1.0	5.2±0.2	5.2±0.2	9.0±1.2	3.8±1.0	0.86±0.1	7.0±0.3
FB48	17	6.2±1.3	**6.5±0.8*****	**4.6±0.8***	**14.1±0.2*****	**9.5±0.9*****	0.9±0.2	**9.3±0.2*****
Ranier	11	**4.9±1.0** ·	18.0±4.8	4.0±0.5	**19.2±2.8***	**15.1±3.1****	**0.6±0.1*****	**9.5±0.3*****
copy of Ranier	13	6.7±1.7	15.3±3.4	4.0±0.6	16.0±2.9	11.9±2.8	0.88±0.1	7.4±0.2
Calvin	9	6.4±0.7	**18.6±3.3** ·	**6.2±0.7*****	18.8±3.3	12.6±3.7	**0.54±0.2*****	**8.7±0.3*****

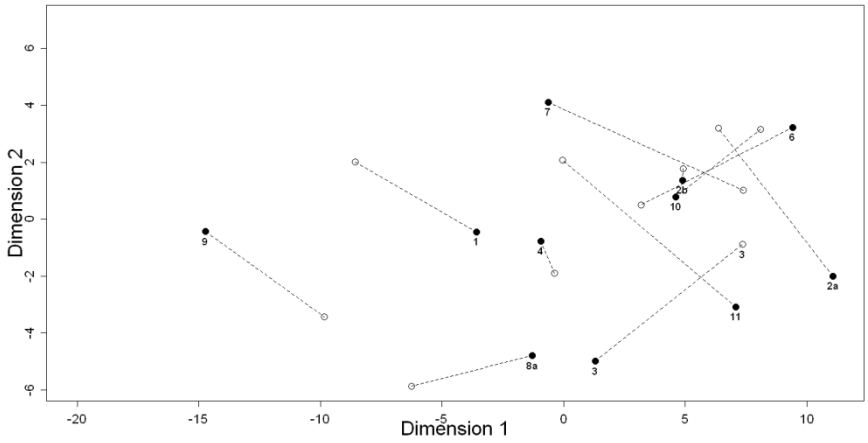


Figure 5.5. Acoustic parameter differences. Multidimensional scaling plot based on all acoustic parameter measurements. The dotted lines join signature whistle copies (black circles) with the original signature whistles (open circles). Numbers correspond to pairs of animals as given in Table 5.1 (see also Table 5.3).

Individuals varied in the parameters modified; on average 4.4 parameters (range: 1-6) differed significantly between the copy and the original signature whistle. Copies most frequently differed from the original (for 10 out of 11 copiers) in mean frequency and maximum frequency (Table 5.3). Over half of the copiers also produced copies that differed significantly from the original signature whistle in end frequency (6 of 11 copiers) and frequency range (7 of 11 copiers). The copies were equally likely to be higher or lower in frequency than the original. In addition to frequency parameters, one adult male, FB26, altered the number of loops in a multi-looped whistle in his copies of the signature whistle of his alliance partner, adult male FB48. Although FB48 varied his number of loops (range: 3-6), FB26 almost always produced a 3-looped copy. The number of loops in FB26's copies and FB48's originals differed significantly (Mann-Whitney: $W = 152.5$, $N_1 = 38$, $N_2 = 35$, $p<0.0001$). All of the signature whistle copies also differed significantly from those of the copiers' own signature whistles in some parameters (mean number of parameters different = 3.54; range: 1-7) while other parameters of a copy resembled those of the copier's own signature whistle (mean = 2; range: 0-5).

5.3.3 Vocal Matching

Vocal matching can be described as a receiver responding to a signal by changing some features of its own vocal behaviour in order to imitate the preceding signal. Bottlenose dolphins have high vocalisation rates during capture-release events (Esch et al., 2009), (Figure 5.6), so it is difficult to judge whether whistles are produced in response to those of other animals. An investigation into the timing of signature whistle copies however revealed that the mean time between an original signature whistle and its copy was significantly less than the mean time between an original signature whistle and a copier's own signature whistle (0.94 sec vs. 2.55 seconds; permutation, $p < 0.0001$; Figure 5.4b). In the long-term captive males, vocal rates were lower, and the matching pattern was clearer: virtually all copying events occurred within 1 second after the emission of the original signature whistle by its owner.

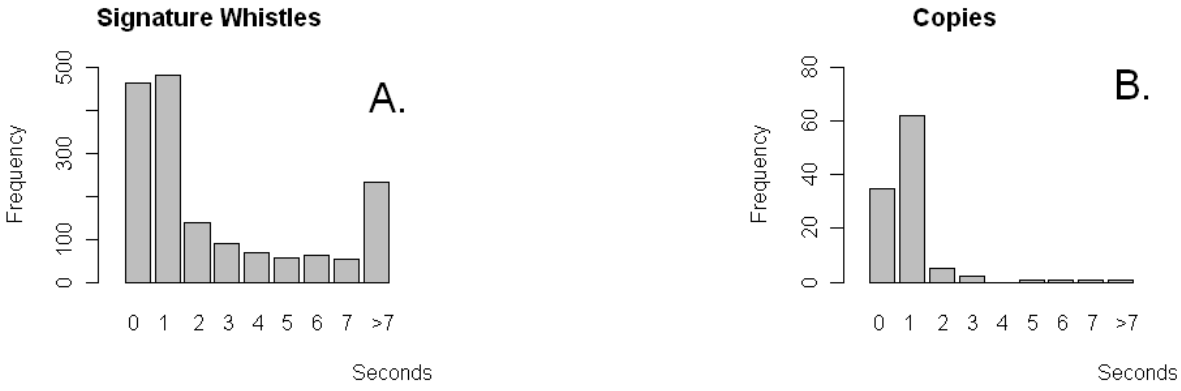


Figure 5.6 - Timing of signature whistle copies. A. The time in seconds between two animals producing their own signature whistles (n=1651). **B.** The time in seconds between the signature whistle owner calling and the signature whistle copy being produced (n=108). Gaps were measured from the end of one whistle to the beginning of the next. A time of 0 seconds indicates overlapping whistles.

5.4 Discussion

These results provide the first evidence of how signature whistle copies are used. A large-scale analysis was conducted on the occurrence of vocal copying in temporarily-caught, wild bottlenose dolphins. This dataset offered a unique opportunity to study the vocal interactions between individuals whose vocal repertoires (Sayigh et al., 2007; Sayigh et al., 1990) and association patterns have been well documented over decades in the wild (Wells, 2003; Wells et al., 1987). The development of bottlenose dolphin signature whistles is influenced by vocal production learning (Fripp et al., 2005; Miksis et al., 2002; Tyack & Sayigh 1997) and individuals use these whistles when separated from their social group (Caldwell et al., 1990; Sayigh et al., 2007; Janik & Slater 1998). Occasional signature whistle copying has however been observed in captive (Janik & Slater 1998; Tyack 1986; Nakahara & Miyazaki 2011) and wild individuals (Tyack & Sayigh 1997; Tyack 1999). In line with previous studies (Janik & Slater 1998; Nakahara & Miyazaki 2011; Janik 2000), whistle copying was found to be rare. This is consistent with the idea that signature whistles are used to indicate identity, since such a system would not be sustainable with high copying rates. Frequent copying of signature whistles would render the identity information of the whistle unreliable. The rare copying of signature whistles may, however, be particularly suited to addressing close associates (Janik & Slater 1998; Janik 2000; Tyack 1991).

Many of the copiers were mother-calf pairs, with both equally likely to copy one another. While most female calves' signature whistles are distinct from their mothers', males sometimes do sound like their mothers (Sayigh et al., 1995). The signature whistles of the male calves in this study however did not resemble those of their mothers (Figures 5.1 and Appendix 1). Signature whistles of male alliance partners also tend to become more alike as they form the alliance (Smolker & Pepper, 1999; Watwood et al., 2004). In this study, however, males continued producing their own, non-identical, signature whistles as well as copying the finer details of each

other's preferred whistle type. Thus, neither age, sex nor relatedness were significant factors for the results presented here.

All pairs of animals that produced signature whistle copies were close associates, with only one pair having a low CoA (0.07) for the year prior to recording: the males FB20 and FB114. These males were, however, each other's closest associate in the 4 year period prior to the recording, with a CoA of 0.33. With their next closest associates they shared CoAs of less than 0.2. This pair may have been "trying each other out" as potential alliance partners in the period leading up to the capture-release. Male alliances are frequently found in the bottlenose dolphin social system (Connor 2002), and once formed can remain stable for many years (R.S. Wells 2003). The other wild male-male pairing in our data set, FB26 and FB48, shared a strong alliance, with a CoA of >0.50 (Watwood et al., 2004).

In animals that are capable of vocal learning, variations can be introduced into a copied signal, allowing encoding of additional information. Bottlenose dolphins produced accurate copies of the frequency modulation pattern of a whistle (Figure 5.1), but introduced fine-scale differences in some acoustic parameters (Table 5.2, Figure 5.5). As a result, signature whistle copies were clearly recognisable as such. Copies may even carry identity information of the copier, as some individuals maintained some frequency parameters of their own signature whistles in their copies (Table 5.3). While these variations may appear subtle, dolphins are clearly capable of detecting such differences at the fundamental frequency as well as at the upper harmonics (Harley 2008; Thompson & Herman 1975). Hence, these copies were unlikely to have been used in a deceptive manner. Only animals that are familiar with the whistle of the owner would, however, be able to recognise copies as copies vs. the original signature. In encounters with unknown animals a high rate of copying would still lead to confusion, arguing for low rates of copying overall.

It is unclear whether the introduced variation in a copy occurs in all whistle copies or just in signature whistle copies. Three lines of evidence however suggest that dolphins can use learning to introduce predictable variation in their copies. First, bottlenose dolphins are capable of producing almost perfect copies of model sounds (Richards et al. 1984). Thus, it does not appear to be a limit on copying performance. Second, in experimental copying studies, bottlenose dolphins sometimes alter parameters of copies from one session to the next, and then only produce copies with these novel parameter values from then on (Sigurdson 1993). Third, it has been shown that some dolphins introduce novel components such as sidebands to whistle copies, while they are perfectly capable of producing whistles without sidebands at these frequencies (Tyack 1986; Tyack 1991). Thus, it is unlikely that variations introduced to copies are merely errors or reflect limitations in copying performance.

Signature whistles are most commonly produced when animals are not close together (Janik & Slater 1998). For parts of the capture-release sessions, animals were moved individually out of the water onto a platform. This involuntary separation of the animals can result in a stressful situation. It also results in a significant decrease in the received level of conspecific whistles for dolphins between the platform and the water, which may simulate an increase in distance between the animals. Similarly, two of the captive males that were close associates in a group of four males produced most of their copies when physically separated from one another. Since signature whistle copying only occurred between closely associated animals in non-aggressive contexts between the four captive males, it can be concluded it is primarily an affiliative signal. In all settings, vocal copying occurred when animals were physically distant from one another. Vision and olfaction, two other senses important in mammalian communication, are either limited (vision) or absent (olfaction) in delphinids in their aquatic environment. Instead, affiliated animals may use signal copying, allowing them to maintain contact with one another at a distance. This contrasts with the

use of song type matching, where it appears to be primarily agonistic (Searcy & Beecher 2009). Bottlenose dolphins primarily use pulsed sounds in aggressive interactions (Overstrom 1983). Copying could play a role in these, but this has not yet been investigated.

A role of vocal copying in group cohesion and the maintenance of social bonds appears to be established in a number of social species (Balsby & Scarl, 2008; Balsby & Bradbury, 2010; Boughman, 1998; Jones & Ransome, 1993; Knornschild et al., 2010; Mitani & Gros-Louis, 1998; Poole et al., 2005). In experimental work it has been shown that bottlenose dolphins can be trained to use vocal copies of novel, arbitrary sounds to refer to objects (Richards et al. 1984). It is not yet known whether they use learned signals in this way in their own communication system. This study has shown that they use copies of learned, individually distinctive signature whistles which could refer to other individuals.

Three cases were also found in which copying of non-signature whistles occurred among females that did not tend to associate much with each other, which hints at a wider relevance of copying in the bottlenose dolphin communication system. Future studies should look closely at the exact context, flexibility and role of copying in a wider selection of species to assess its significance as a potential stepping stone towards referential communication.

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Chapter 6

To copy or not to copy: the function of signature whistle copying in the Bottlenose Dolphin (*Tursiops truncatus*)

6. 1 Introduction

Signal copying is a behaviour observed in a number of species including birds (Falls & Krebs 1975; Krebs et al., 1981; Falls 1985; Beecher et al., 2000), elephants (interspecific; Poole et al., 2005), bats (Jones & Ransome 1993; Knornschild et al., 2010), and cetaceans (Janik 2000; Miller et al., 2004; Noad et al., 2000). In passerines and odontocetes, signal acquisition is heavily influenced by vocal learning (Janik & Slater 1997; Catchpole & Slater 2008). Vocal production learning enables animals to copy novel sounds in their environment and develop their own individually distinctive repertoire of calls (Janik & Slater 2000). The development of large repertoires or individually distinctive calls in vocal learners may have selected for the use of copying skills.

The copying of individually distinctive calls may allow conspecifics to label or address one another (Tyack 1993). Vocal labeling or naming of social companions is a foundation of our own communication system. We form individual bonds, maintain associations and learn new acquaintances by learning people's names and use them in social interactions as a way of addressing and soliciting that person's attention. Each person has a name that becomes a referential signal associated with that individual. The naming or labeling of social companions is, however, notably rare in the animal kingdom. Most surprisingly it is absent in nonhuman primates, who are able to label objects gesturally but not with novel acoustic signals (Janik &

Slater 1997). Instead we see this ability to use vocal labels in both captive parrots (Pepperberg 1981; Wanker et al., 2005) and captive dolphins (Richard et al., 1984). There is evidence that the contact call in spectacled parrotlets (*Forpus conspicillatus*) is referential (Wanker et al., 2005), meeting both production and perception criteria (Evans 1997; Macedonia & Evans 1993). It is not yet known, however, whether signature whistles are used as social referents in the natural communication system of the bottlenose dolphin.

Bottlenose dolphins are particularly interesting due to their individually distinctive signature whistles (Caldwell & Caldwell 1965; Caldwell et al., 1990; Sayigh et al., 2007) that develop under the influence of vocal learning (Tyack & Sayigh 1997; Miksis et al. 2002; Fripp et al., 2005). Signature whistles contain identity information independent of general voice features (Janik et al., 2006). Instead of relying on morphological differences in the vocal tract, dolphins can encode identity in the unique frequency modulation pattern of their signature whistles (Janik et al., 2006). These whistles are developed by each individual through vocal learning, and it has been proposed that they may be used as vocal labels (Tyack 1993; Janik 2000). Signature whistles function as contact calls, pertaining to both individual identity and to maintaining group cohesion (Janik & Slater 1998; Sayigh et al., 1999). Their use in wild animals constitutes roughly half of their tonal whistle vocalisations (Buckstaff 2004; Cook et al., 2004; Watwood et al., 2005); therefore comprising an important part of their vocal repertoire.

We know signature whistles form a stable component of an individual dolphin's vocal repertoire (Sayigh et al., 1990), at the same time these animals are capable of substantially modifying their vocalisations through vocal production learning. This ability is maintained throughout their adult life (Richards et al., 1984). Their capability for this skill means that the signature whistle of one animal may be found as a minor part of the vocal repertoire of other individuals (Janik & Slater 1998; Tyack 1986; Tyack 1991), evident as occasional events of

whistle copying or matching (Tyack 1991; Tyack & Sayigh 1997; Janik & Slater 1998; Janik 2000). Animals are capable of producing adequate copies of novel sounds, even after only one exposure to the sound (Richards et al., 1984). Therefore the copying of another dolphin's arbitrary signature whistle could occur between all members of a population, including those that are not familiar with one another. I have, however, already shown that signature whistle copying in bottlenose dolphins primarily occurs between closely bonded animals (Chapter 5).

It has been hypothesized that signature whistles may be used as referential signals amongst conspecifics (Janik et al., 2006; Tyack 1993) . Captive dolphins have demonstrated their ability to use novel, learned signals to referentially label objects (Richards et al., 1984). Tyack (1993) proposed the *signature labeling hypothesis*; where by imitating the signature whistle of a conspecific the imitator is initiating an interaction with said conspecific, essentially *addressing* the animal. Bottlenose dolphins have been reported to occasionally copy the signature whistles of absent conspecifics (Watwood et al., 2005), perhaps calling them by 'name'.

In this chapter, I aimed to address the question of whether animals can be addressed by their signature whistles. I conducted playback experiments with wild, unrestrained bottlenose dolphins. If animals can be addressed by their signature whistles, I would expect an animal to reciprocate vocally (by repeating its signature whistle) when it hears an imitation of its signature whistle. To test this I performed focal follows and recorded signature whistles *in-situ* of the animals in my focal group. I then either played back the signature whistle of one of the animals I had just recorded, thereby producing a copy and '*addressing*' the animal, or I played back a control whistle of an unfamiliar animal from a different population. Finally, I quantified the similarity of whistles from the focal group after the playback, to the playback stimuli. By observing the response of the focal group we may begin to realize whether signature whistles can be used as referential labels or 'names'.

6.2 Methods

6.2.1 Study Site

The study was conducted in St Andrews Bay off the northeast coast of Scotland between Montrose and Fifeness during May and September 2010. The subjects comprised a resident population of bottlenose dolphins that range between the Moray Firth and St Andrews Bay (Wilson et al., 1999; Wilson et al., 2004). Group follows were conducted in a small 6m boat at sea state 3 or less. Once a group of animals were encountered, they were approached and photo-identification was carried out on each group member. In order to conduct a focal group follow I chose relatively well-marked animals. Every individual was photographed using a Canon Digital D30 SLR camera with a Sigma 100-300mm, F4 zoom lens. If group composition changed with ≥ 1 animal(s) either leaving or joining the group then spacer photographs were taken and the group was re-photographed.

Acoustic recordings of the focal group were taken using two HTI-96 MIN hydrophones (frequency response: 0.002 to 30 kHz ±1 dB) towed at 2m depth. Recordings were made on a Toshiba Satellite Pro Laptop using an Edirol UA-25 with a sampling rate of 96000 Hz, 16 bit digitisation. The recordings were continuously monitored on the boat using real-time spectrogram displays in Adobe Audition v2.0 (Adobe Systems). This enabled signature whistles produced by the focal group to be identified *in-situ*. Signature whistles were identified by their temporal and stereotyped patterning using the SIGID method (Janik et al., in press). The SIGID method uses the stereotypy and temporal patterning, which are unique to signature whistles, to identify them in wild free-ranging groups of animals. The authors show that signature whistles occur in bouts, where they are produced within 1-10 seconds of each other (Janik et al., in press). This is distinctly different from non-signature whistles, which occur over longer or shorter periods. For

SIGID to identify whistles as signature whistles, whistles of the same type must be produced in a sequential bout containing at least 4 whistles with 75% or more occurring within 1- 10 seconds of at least one other whistle within that bout (Janik et al., 2012). An example of an identified signature whistle type is given in Figure 6.1. Since it is difficult to perform this analysis in real time, the SIGID method was re-run in the laboratory and only those playbacks in which the results were confirmed were included in the analysis. I remained close to the focal group during the follow and all other animals in the area were noted. If another group of animals was sighted within 300-400m I did not conduct a copying playback as I could not be sure the signature whistles I recorded *in-situ* were from the focal group.

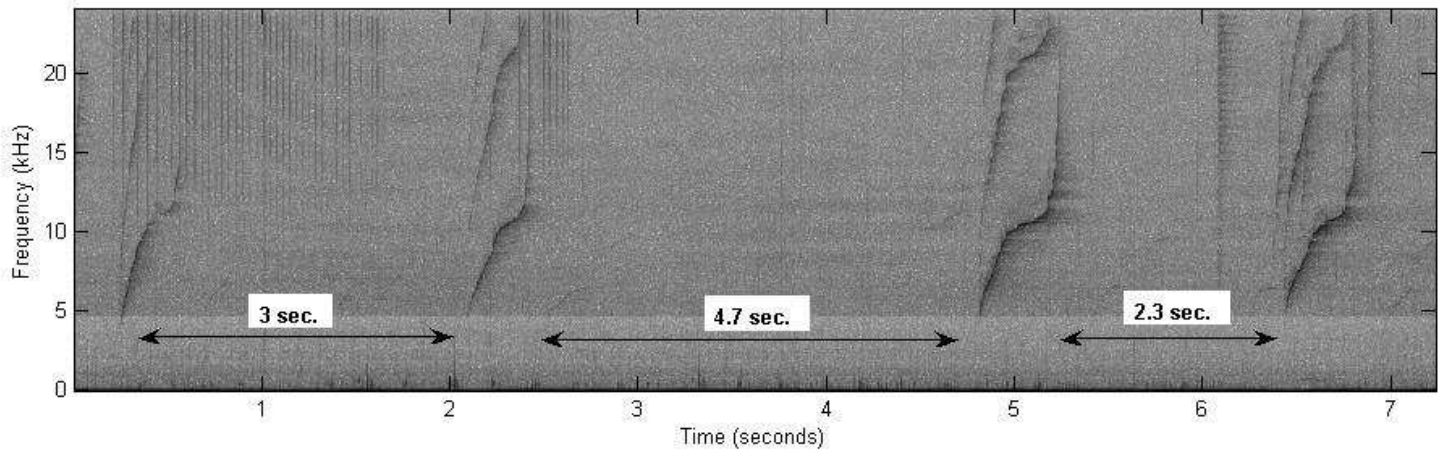


Figure 6.1. A signature whistle type recorded in St Andrews Bay on 16th August 2010. The signature whistle was identified using the SIGID method (Janik et al., in press). All four whistles occur within 1- 10 seconds of at least one other whistle of the same type.

Once a signature whistle sequence had been identified the real-time recordings were stopped and a synthesized version of the identified signature whistle was produced using SIGNAL v 4.0 (Engineering Design, Berkeley, CA), (see method in Janik et al., 2006). Synthetic versions of unfamiliar signature whistles of isolated, captive animals from Zoo Duisburg,

Germany (2 captive born / 2 wild caught in Gulf of Mexico), and the Living Seas, Epcot, Florida (1 captive born / 1 wild caught in Gulf of Mexico), acted as controls. I ensured that average sound pressure levels were the same by standardising whistle RMS amplitude across files.

6.2.2 Playback Protocol

The playback trials for both treatments consisted of a 2 whistle playback sequence. The playback began with a synthetic whistle followed by 3 seconds of silence and ended with another repetition of the same synthetic whistle. The playback was conducted when all members of the recorded group were present. To make sure that the animal who emitted the playback whistle remained with the focal group, the playback was aborted if any animals were deemed to have left the group during the synthesis of the signal.

During playbacks the boat was stopped and the engine was turned off. Acoustic recordings were made with four HTI-96 MIN hydrophones (frequency response: 0.002 to 30 kHz ±1 dB) distributed around the boat in a rectangular formation and were placed between 220cm and 240cm apart; all four were at a 2m depth. Recordings were made on a Toshiba Satellite Pro laptop using a 4 channel Avisoft 416 UltrasoundGate through Avisoft RECORDER v3.4 (Avisoft Bioacoustics, Raimund Specht, Berlin; frequency response: 0.02 – 370 kHz ± 3 dB) with a sampling rate of 100000 Hz, 8 bit digitisation. A Lubell LL916 portable underwater speaker (Lubell Labs Inc, Columbus, Ohio; frequency response: 600 Hz-21 kHz ±8dB) connected to a Magnat classic 1000 XL car amplifier (frequency response: 0.005 – 100 kHz ± 3 dB) was placed at a 2m depth on the port side once the boat was stationary. Stimuli were played back from a Toshiba Satellite Pro laptop using the Avisoft 416 Ultrasoundgate with Avisoft RECORDER v3.4 (Avisoft Bioacoustics, Raimund Specht, Berlin; frequency response: 0.02 – 370 kHz ± 3 dB). The source level was set to ~150 ± 3 dB re 1 µPa at 1m (rms).

Bottlenose dolphins have been shown to have higher vocal rates when more dispersed than during coordinated surface travel (Quick & Janik 2008). Playbacks were therefore conducted when the focal group was participating in a non-polarised behaviour or were socialising, where the use of signature whistle copying may be more likely to occur.

The behaviour and location of the focal group were monitored both before and after the playback. The following variables were duly noted; distance, position, orientation and surface behaviour of members of the focal group. The positioning was based on a clock face with 12 o'clock at the bow of the boat. The distances of the animals from the boat were estimated by eye and corroborated when possible with laser range finders (Bushnell Scout 1000: +/- 1m accuracy) with precision estimates by eye within ± 10m. Initial distances were measured prior to the playback trial. The mean distance to the dolphin group at the time of playback was 80m (range: 15m – 300m). There was no difference in distance to the group at the time of playback between the two treatment types (t test: $t = 0.2946$, $df = 17$, p-value = 0.77). Upon completion of the playback trial, the behaviour of the focal group was monitored for a minimum of 6 surfacings. The distance of the closest animal to the boat before and after the playback was used to determine a directional movement response (+/-) of the animals to or from the boat.

6.2.3 Additional Data

Data was also analysed from 2001, where playback experiments were conducted at the boundary between the Moray Firth and the Cromarty Firth, northeast coast of Scotland. The study subjects were the same population of bottlenose dolphin that range from the Moray Firth to St Andrews Bay (Wilson et al., 1999; Wilson et al., 2004). A total of 5 playback experiments were conducted

by V. Janik across 5 different days between the 12th June and the 15th August 2001. Animals were recorded from a small, stationary research vessel using two HTI 94 SSQ hydrophones (frequency response: 0.002 to 30 kHz ±1 dB), and a Tascam DAP1 DAT recorder sampling at 48 kHz (frequency response: 0.02 to 22 kHz ± 0.5 dB). Recorded whistles were used as playback stimuli. Playback stimuli were not synthetic, and consisted of either a 1 whistle playback (n=2) or a 2 whistle playback sequence with 3 seconds of silence separating the whistles (n=3). The SIGID method (Janik et al., in press) was used to determine whether these whistles were signature whistles of the animals present. The movement response of the animals was recorded with a Sony Digital 8 Handycam from an elevated shore-based position. No photo-identification was available for this dataset.

6.2.4 Analysis

The acoustic recordings were analysed by inspecting the spectrograms (FFT length 1024, 87.5% overlap, Hanning window) in Adobe Audition v2.0 (Adobe Systems). All statistical procedures were conducted in R (R project for statistical computing; GNU project). In order to identify if animals responded to the playback treatments, the whistle contours (frequency modulation patterns) of the playback stimuli and the subsequent vocal responses of the animals were rated on a similarity scale by 5 human observers. Visual classification has been shown to be more reliable than computer-based classification, and is widely used in animal communication studies (Catchpole & Slater 2008; Janik 1999; Sayigh et al., 2007). The human observers were all experienced in sound analysis and blind to context and animal identity. They were given the extracted contours of the whistles as frequency versus time plots and were asked to rate whistle similarity using a 5-point similarity index ranging from 1 (not similar) to 5 (very similar). The kappa statistic was used to ascertain observer agreement (Siegel & Castellan 1988). The

observers showed statistically significant agreement on their similarity ratings (Kappa Cohen = 0.47, $z = 24.4$, $P < 0.0001$ (Siegel & Castellan 1988)).Whistles that received an average similarity score of ≥ 3.6 were deemed to be a vocal copy; whereby an animal responded to the playback stimulus by replying with the same whistle. A value of 3 indicates a relatively high similarity as indicated in previous studies (Watwood et al., 2004; Janik 2000), with one study using an even higher value of ≥ 3.6 (Sayigh et al., 1995). Although a value of ≥ 3 is the commonly used value representing high similarity, the more conservative value (≥ 3.6) was chosen because if the signature whistle owner responds to the playbacks by producing its signature whistle, very high levels of similarity are expected.

A Barnard's exact test was used to compare the animal's vocal responses to the playback treatments. The vocal responses were classified as copies or non-copies, as decided by the human observers. Barnard's test is used as it is more powerful than Fisher's Exact test. This is because the discrete nature of Fisher's exact test means it produces highly conservative p values for small sample sizes. Whistle rates of the group of animals (rate per individual per min) were compared before and after playback treatments, and between treatments. A Lilliefors (Kolmogorov-Smirnov) test was used to test for normality followed by a t-test or a Wilcoxon test with a Bonferroni--adjusted significance level of $p < 0.0125$. The same tests were also performed on the movement response using a significance level of $p < 0.05$.

6.3 Results

I conducted a total of 24 successful playbacks (copy = 12, control = 12) across 30 days between 17th May and 2nd September 2010. A total of 2 control playbacks were discarded due to bad recording quality. In addition, 2 copy playbacks were not confirmed as signature whistles using the SIGID method. This left a total of 20 playbacks; 10 copy playbacks and 10 control playbacks (Table 6.1). The SIGID method was also applied to the Cromarty Firth data, only 2 out of the 5 whistle stimuli were confirmed as signature whistles and thus used in further analysis.

In total 95 whistles (control treatments = 41, copy treatments = 54) were recorded within the first minute following playback trials in St Andrews Bay. Of those, 7 were deemed to show high similarity (mean similarity score $\geq$ 3.6) with the playback stimuli. All high-similarity whistles occurred during signature whistle playbacks where one of the signature whistles of the animals in the target group was played, and where subsequently an animal produced the same whistle. These 7 whistles were from across 4 different playback trials. For the two playbacks conducted in the Cromarty Firth, 14 high quality whistles occurred within a minute of the two playback trials. Of those, 12 were deemed highly similar to the playback stimuli (mean similarity score $\geq$ 3.6). These 12 whistles were from across both playback trials.

Dolphin group sizes for the playbacks varied with a mean group size of 13.2 (range: 3-25) for the control playbacks and 13.2 (range: 3-23) for the copy playbacks. There was no difference between the mean group size for the two treatment types (t test: $t = 0.18$, $df = 17$, $p > 0.8$).

Table 6.1. Summary for each of the playback treatments; including number of animals in the group at the time of playback, the whistle rates in the 1 minute before (pre) and after (post) playback, the difference in distance of the closest animal measured before and after playback, and whether animals called back with the same whistle (copy).

Treatment	Group Size	Whistle Rate Pre (#/min/individual)	Whistle Rate Post (#/min/individual)	Movement Response (meters)	High Similarity Whistles (vocal reply)
Control 1	8	0.187	0.5	-40	0
Control 2	5	0.8	0.6	-55	0
Control 3	10	0.3	0.3	+30	0
Control 4	24	0.0	0.0	- [$]	0
Control 5	-	-	-	-30	0
Control 6	11	0.18	1.72	0	0
Control 7	25	0.32	0.04	-30	0
Control 8	25	0.28	0.0	-180	0
Control 9	8	0.625	0.5	+140	0
Control 10	3	0.0	2.33	-180	0
Treatment 1	21	0.9	0.0	+35	0
Treatment 2	22	1.22	0.59	+30	0
Treatment 3	5	0.4	0.0	-10	0
Treatment 4	9	0.0	0.4	+30	0
Treatment 5	23	0.26	0.13	0	0
Treatment 6	11	0.0	0.45	-70	1
Treatment 7	10	1.1	1.1	-70	2
Treatment 8	3	1.67	3.3	+150	3
Treatment 9	4	0.0	1.0	+20	1
Treatment 10	17	0.0	0.23	-30	0
Additional 1	-	-	-	-20	7
Additional 2	-	-	-	- [$]	5

[$] Equipment failure meant movement response was not available for these playbacks

A total of 6 playbacks out of the combined total of 22 resulted in animals responding by calling back with the same whistle type. All of these playbacks were of signature whistles recorded from the same group of animals (n=12). In sharp contrast, animals never responded to the control treatments by copying the whistle type used in the control playback (n=10).

When considering only the St Andrews Bay data, the vocal response differed significantly between the two playback treatments (Barnards exact test: Wald statistic = 2.2, N = 20, one-tailed $p < 0.02$, two-tailed $p < 0.04$ (Figure 6.2a)). These results indicate that dolphins are significantly more likely to respond by calling back with the same whistle type when they detect the signature whistle of a familiar group member than an unfamiliar individual. This may be the result of two possibilities: a) the owner of the signature whistle replies when he is 'addressed' or b) another animal hears the signature whistle of an animal it knows and calls back with a copy of that signature whistle. When the Cromarty Firth data is included this difference is heightened (Barnards exact test: Wald statistic = 2.6, N = 22, one-tailed $p < 0.006$, two-tailed $p < 0.02$ (Figure 6.2b)).

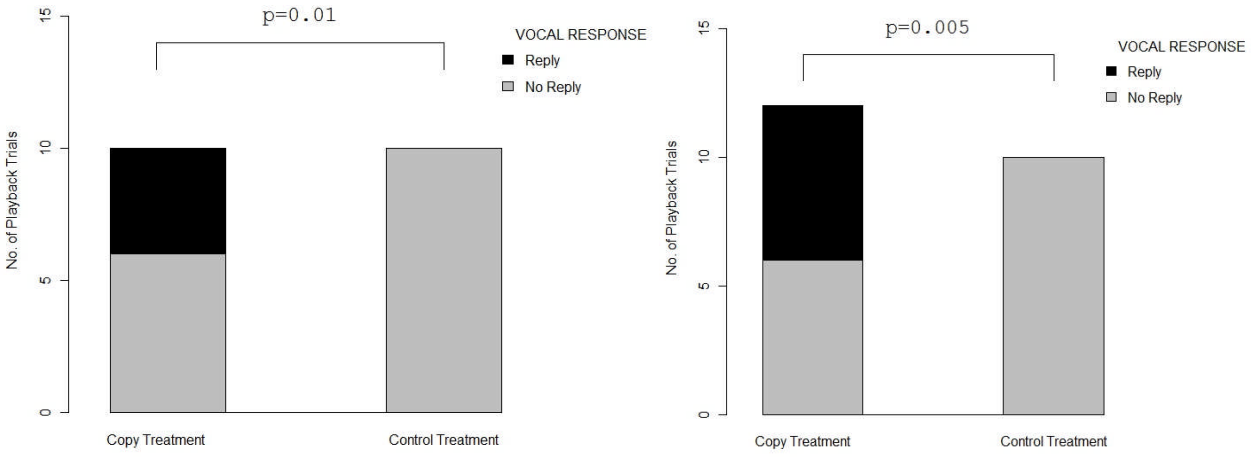


Figure 6.2. A. The vocal response of wild bottlenose dolphins to playbacks of their own signature whistle (copy, n=10) and unfamiliar signature whistles (control, n=10). The response may either be a reply (black) where an animal calls back with the same whistle type, or they may not produce a reply (grey). Comparison made using Barnards Exact test; * < 0.05. B. Same data as A, but the Cromarty Firth data is also included.

It is important to note that for none of the 22 playbacks was the stimulus whistle produced by the animals in the 1 minute preceding the playback (Figure 6.3).

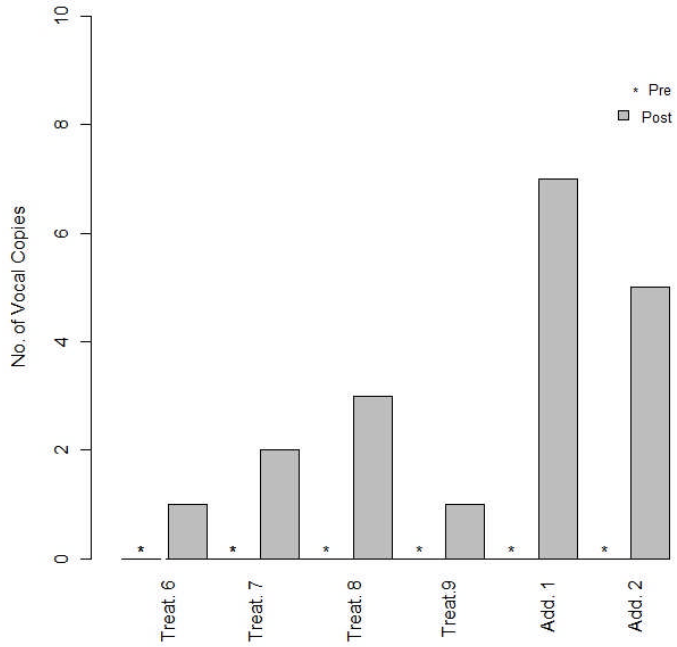


Figure 6.3. For those playbacks where copies were produced in response to the playback stimulus (n=6), this figure highlights the total number of whistles that were the same as the stimulus produced in the 1 minute period before the playback (pre), and 1 minute after the playback (post).

When animals did respond to the playbacks by producing the same whistle, the number of copies they produced varied (Table 6.2). The latency to these responses also varied with one of the responses being fairly delayed (50 seconds). Even if, however, this delayed response was removed from the analysis, the test remained significant.

Table 6.2. The number of vocal copies produced in response to the playbacks (where copies were produced), with the time in seconds to the first copy being produced.

Treatment	Number of Copies in Response to Playback	Time in seconds to First Copy Produced
Treatment 6	1	2.5[$]
Treatment 7	2	50
Treatment 8	3	1.3
Treatment 9	1	1.7
Additional 1	7	1.5[$]
Additional 2	5	8.3

[$] Animal produced first copy after the first whistle in the two whistle playback sequence.

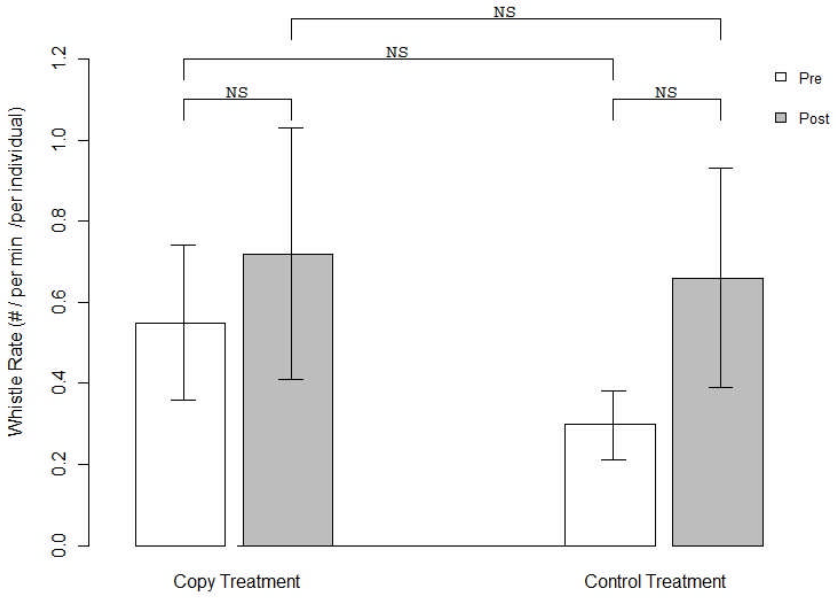


Figure 6.4. Whistle rates per min/individual for both copying (n=10) and control treatments (n=9). The bars represent mean whistle rates for 1 minute pre playback (white) and 1 minute post playback (grey) with standard error bars.

Overall there was no difference in the rate of vocal response to the playbacks between the two treatments for the St Andrews Bay data (t test: t = -0.1496, df = 17, p-value = 0.88 (Figure 6.4)). Neither was there any difference in the vocal rate prior to playback between the two treatments (t test: t = -1.186, df = 17, p-value = 0.25 (Figure 6.4)). There was not a significant increase or decrease in vocal rate as a result of the playback for the copy treatments (t test: t = -0.4594, df = 18, p-value = 0.65 (Figure 6.4)) or the control treatments (t test: t = -1.2741, df = 16, p-value = 0.23 (Figure 6.4)). This shows that hearing an unfamiliar whistle from a different population did not suppress their vocal rate. The mean vocal rates with standard errors can be seen in Figure 6.4. The mean latency to first vocal response between the playback treatments did not differ significantly (Wilcoxon test: W = 20.5, df = 12, p-value = 0.7).

Figure 6.5 reveals that the mean movement response for the St Andrews Bay data was positive (6 m) for the copy treatments, i.e. the animals moved closer to the boat, and was negative (-18.3m) for the control treatment i.e. the animals moved further away from the boat. However, overall there was no significant difference in the movement response of the animals to the two different playback treatments (t test: t = -0.72, df = 18, p-value = 0.4). This may, however, be due to small sample size and the large variance in our sample.

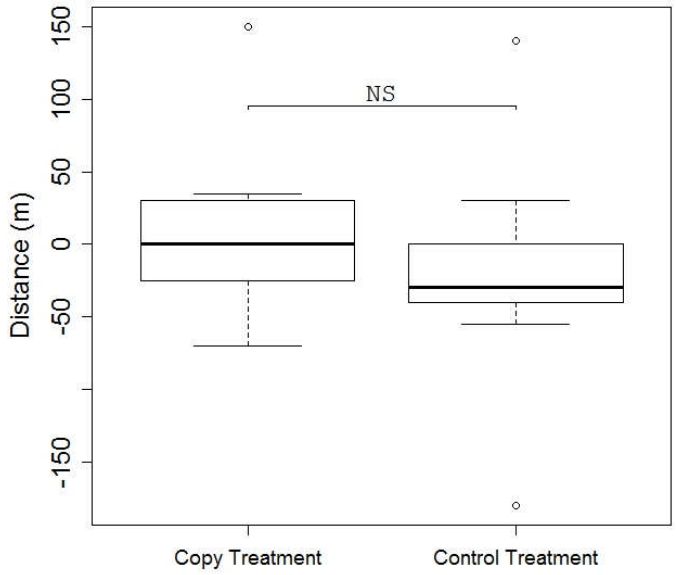
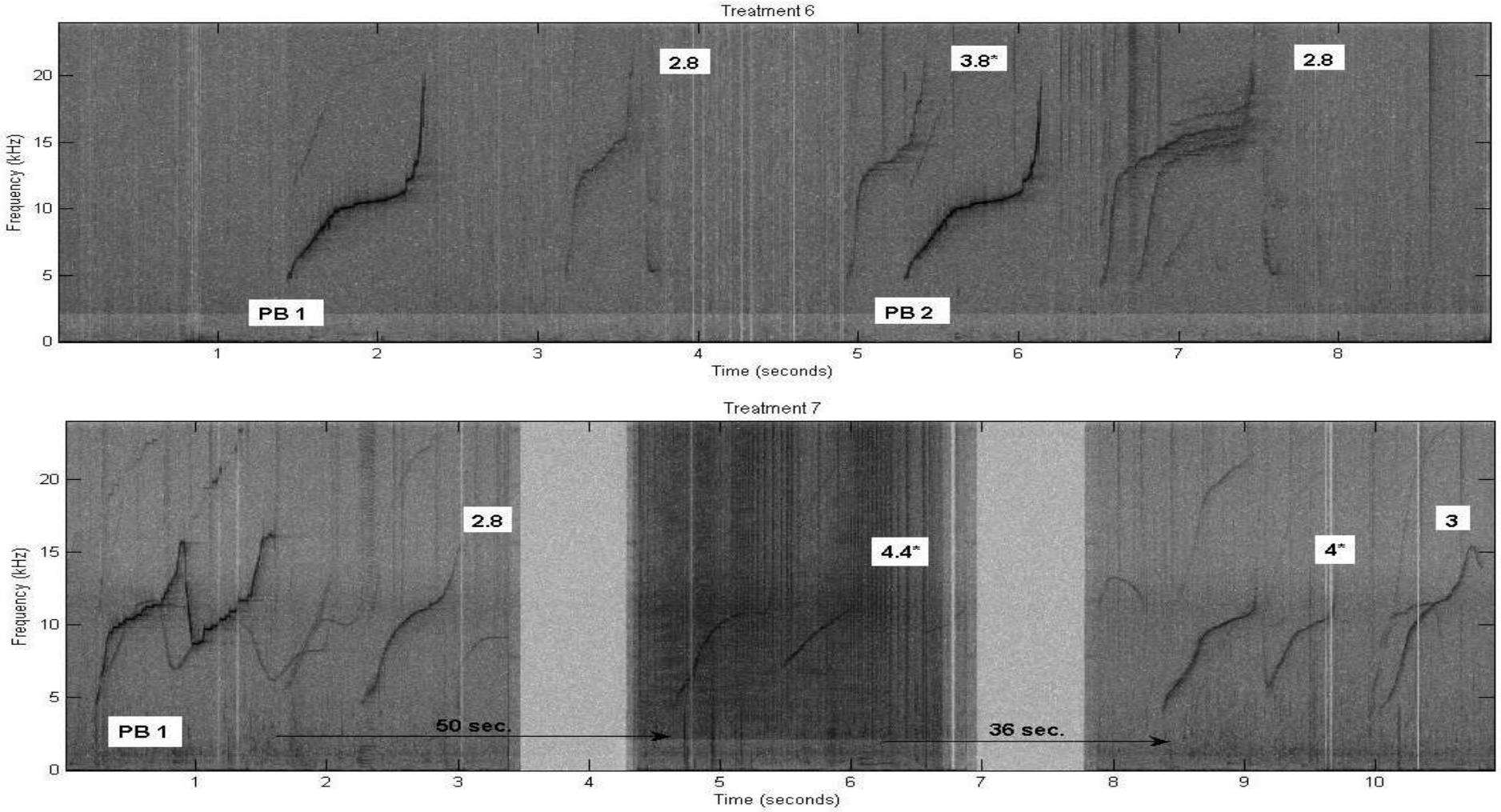
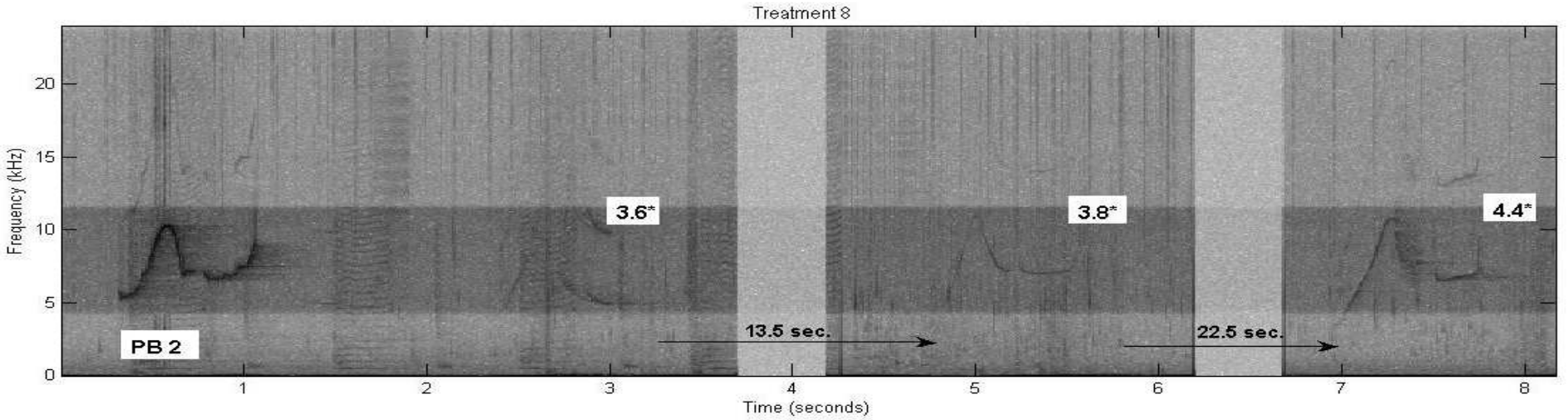


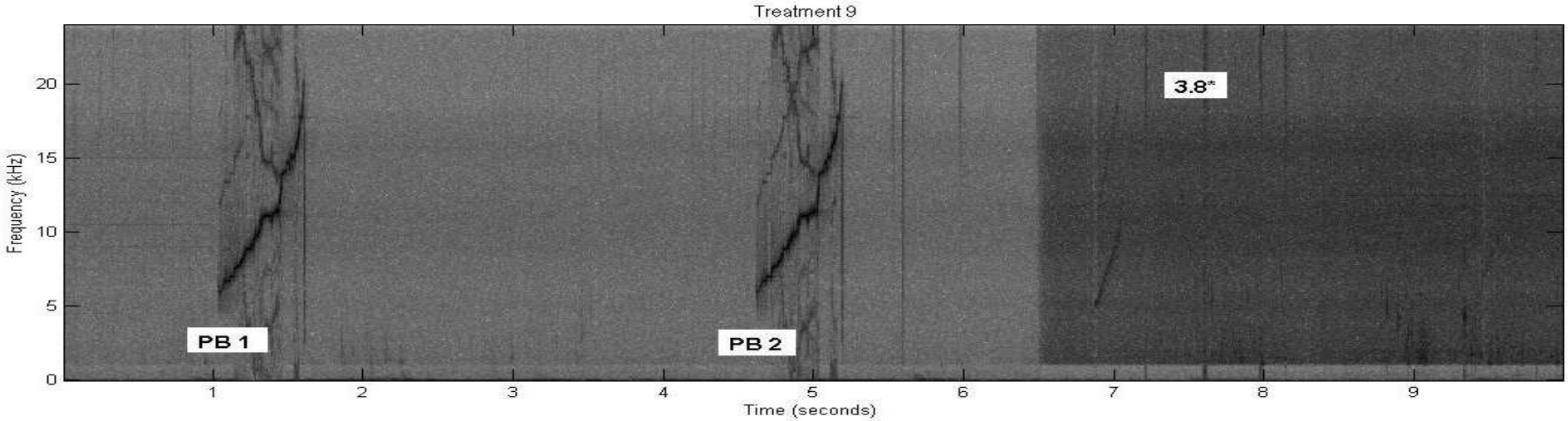
Figure 6.5. Boxplot indicating the movement response (change in distance of closest animal to the boat before and after playback, giving directional movement either away from the boat (-) or towards the boat (+)) for the two treatment types; copy (n=11) and control (n=9).

Examples of vocal responses to both copy playbacks and control playbacks can be seen in figures 6.6 and 6.7 respectively.

COPY TREATMENT




Treatment 8
Frequency (kHz)
Time (seconds)
3.6*
3.8*
4.4*
PB 2
13.5 sec.
22.5 sec.


Treatment 9
Frequency (kHz)
Time (seconds)
3.8*
PB 1
PB 2

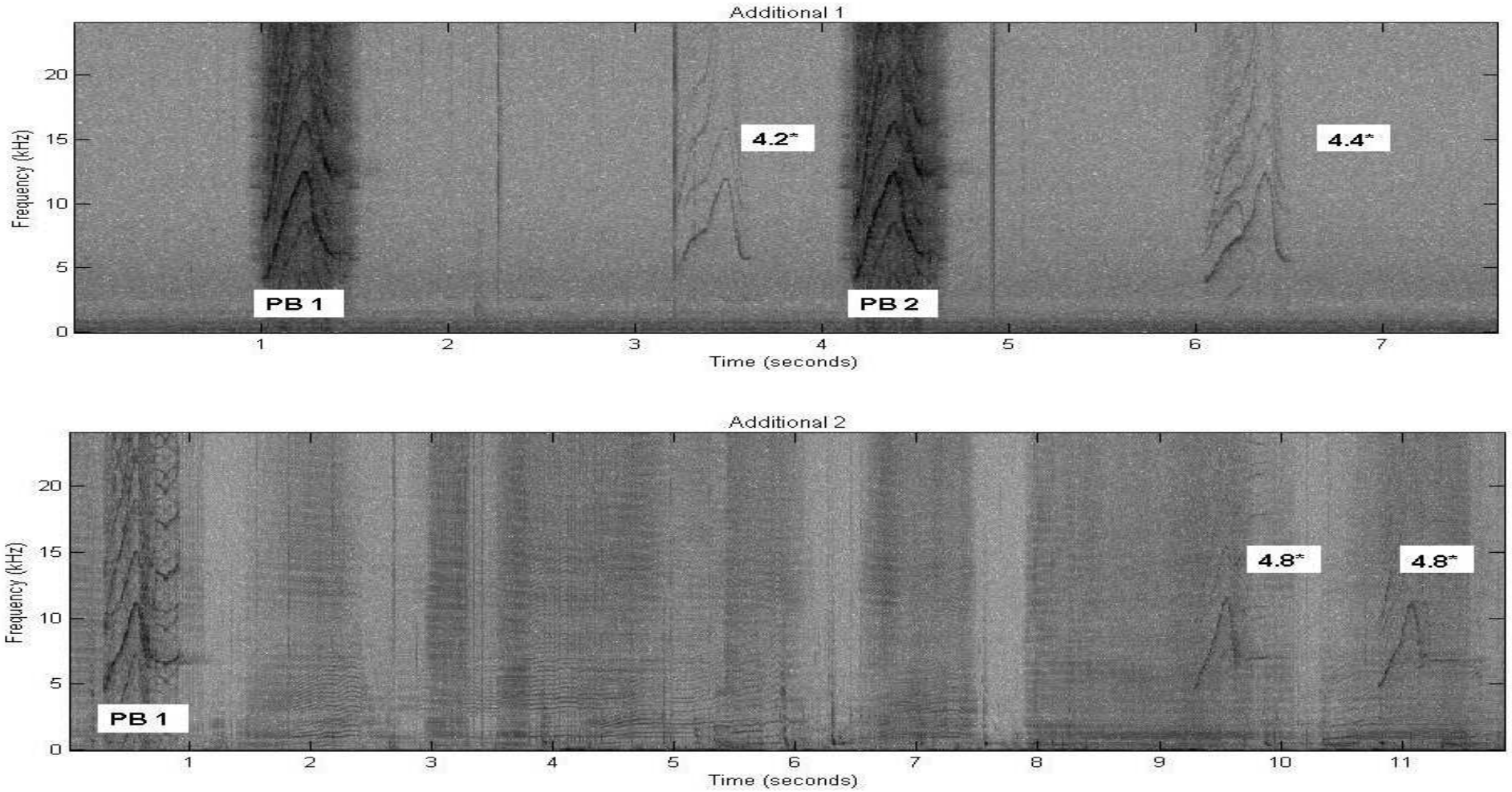
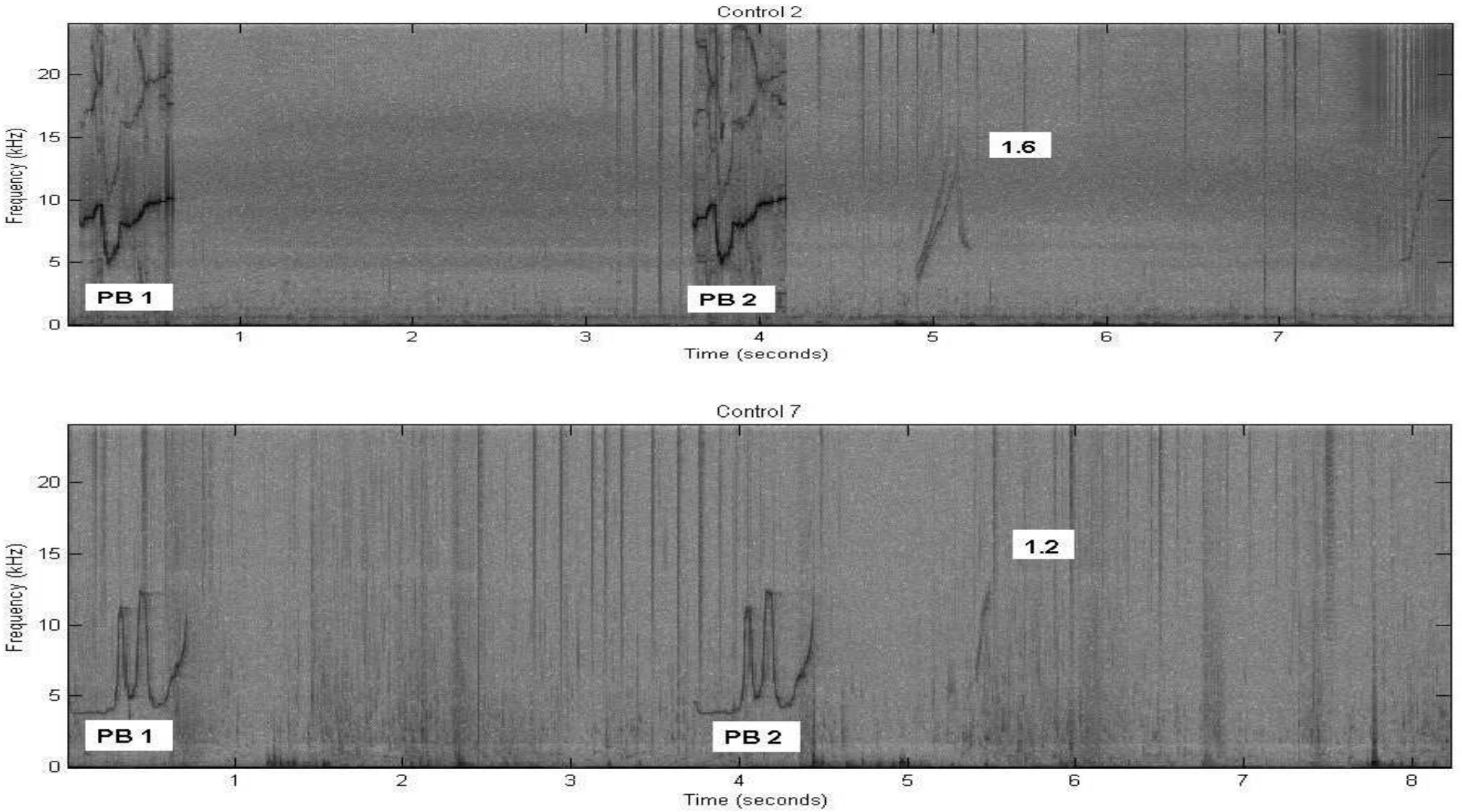


Figure 6.6. Spectrograms of the 6 playbacks where animals called back with the same whistle; sampling rate is 48000 Hz, FFT length 1024, Hanning window function. Playback stimuli are labeled (PB) and the average similarities of the whistles recorded are given, the high similarity whistles (vocal copy) are highlighted (*). If the time between the playback and the response is greater than a few seconds arrows have been inserted indicating the actual time.

CONTROL TREATMENT



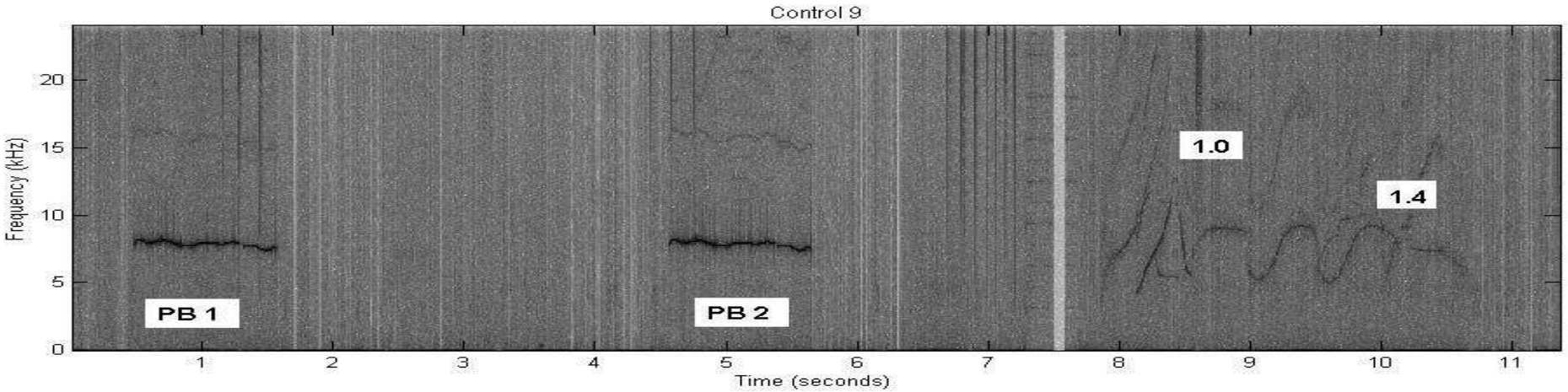


Figure 6.7. Spectrograms of some of the control playbacks; sampling rate is 48000 Hz, FFT length 1024, Hanning window function. If the time between the playback and the response is greater than a few seconds arrows have been inserted indicating the actual time. Playback stimuli are labeled (PB) and the average similarities of the whistles recorded are given.

6.4 Discussion

These results provide the first evidence that wild bottlenose dolphins respond to hearing a copy of their signature whistle by calling back. The results from chapter 3 provided striking evidence from captive animals that signature whistle matching can be used to address individual animals. The results presented in this chapter reveal animals can also address social companions by producing a copying of that animal's signature whistle first. Animals were significantly more likely to respond to the signature whistle of a familiar group member by calling back with the same whistle type. Some of these copies were near perfect representations and likely represent the owner of the signature whistle replying when 'addressed'. Other copies have slight parameter differences to the stimulus used. The differences may represent either a) the signature whistle owner modifying its whistle slightly to indicate it is a response, this is seen in vocal exchanges between squirrel monkeys (Biben et al., 1986), and we know bottlenose dolphin signature whistles contain context-related information as well as pertaining to animal identity (Janik et al., 1994), or b) it is not the owner calling back but another group member who hears the signature whistle of an animal it knows and calls back with a vocal copy of that signature whistle.

The latter is perhaps unlikely as signature whistles are contact calls and we may therefore expect animals to call back with their own signature whistle. Bottlenose dolphins exchange signature whistles when meeting at sea (Quick & Janik, 2012), and vocal copying or matching has not been reported during these interactions. Instead individuals produce their own individually specific signature whistle in a form of greeting sequence, allowing individuals to identify one another. It is therefore unlikely that it is a different animal that responds to our playbacks by producing a copy of the signature whistle, at least not for every playback. Signature whistle copying does occur between affiliated animals (Chapter 5) but remains relatively rare in the

dolphin communication system (Janik 2000; Janik & Slater 1998; Watwood et al., 2005), although significantly above chance levels (Janik 2000). Such rarity of whistle copying may be necessary to preserve the honesty of the signature whistle as an indicator of identity. Frequent copying of signature whistles would render the identity information of the whistle unreliable, especially at distance because fine-scale acoustic cues (Chapter 5) may not be discernible at distance due to the effects of sound degradation. It is therefore likely that the majority of the responses in this study were from the target animal who originally produced the playback whistle, rather than from other group members spontaneously copying the whistle.

Signal copying is evident in other species that use vocal production learning. Songbirds copy songs in vocal matching interactions as a form of territorial defence (Searcy & Beecher 2009). Japanese macaques copy the finer details of another animal's coo call, also in matching interactions, as a way of maintaining acoustic contact (Sugiura 1998). Vocal matching allows individuals to initiate contact with an individual (Janik 2000; Krebs et al., 1981; McGregor et al., 1992; Miller et al., 2004; Sugiura 1998; Todt 1981). Whistle matching in dolphins, where two or more separate individuals produce the same whistle type within a short time window, has been shown in both captive and in wild animals (Janik 2000; Janik & Slater 1998; Miller et al., 2004). Thus, the matching of whistle types seems to be an effective way of addressing individuals (Janik 2000; Tyack 2000; Chapter 3). The results presented here show that vocal matching may not be the only mechanism that allows individuals to initiate contact with a specific animal. None of the 6 successful playbacks had a whistle of the same type as the stimuli produced in the 1 minute period prior to the playback (Figure 6.2). In line with the *signature labeling hypothesis* (Tyack 1993), animals recorded here seemed to respond preferentially to a copy of their signature whistle, as if called by 'name'.

The use of vocal labels to address social companions has also been described in captive parrots (Wanker et al. 2005). They have been found to label conspecifics but each bird does not use the same vocal model for a particular individual. In addition, there is little evidence that wild parrots use vocal labels to label conspecifics (Balsby & Bradbury 2010).

Songbirds are known to respond to hearing songs that are in their repertoire by singing back with the same song known as 'song-type matching' (Bremond 1968; Krebs et al. 1981; Beecher et al., 2000). Birds will show a stronger response to song sung by a stranger than a territorial neighbor (Stoddard et al., 1992). Some species, however, respond to the most similar song irrespective of caller. These responses can be strongest to playbacks of 'self-song' recorded from the focal bird (Falls et al., 1982). These recordings are, however, not synthesised and therefore are difficult to interpret functionally. One interesting difference between birdsong and dolphin signature whistles is their proportion of use in the animal's repertoire. Songbirds encode their identity in their song repertoire with songs used in largely equal proportion. The bottlenose dolphin, however, produces one stereotyped whistle type which can from a minor part of another animal's vocal repertoire as a result of copying, but it only forms a major part of one animal's repertoire, allowing it to be a label for that particular individual.

The playbacks discussed in this chapter did provide some interesting points for discussion. For example there was an extended delay in response time for treatment 7 (Table 6.2), although a partial copy seems to have been produced immediately after the playback (Figure 6.5). Vocal exchanges in animals appear to be governed by temporal associations allowing animals to discern between a reply and a call produced at random (Nakahara & Miyazaki 2011). A long delay may not necessarily be in response to the playback stimuli. Call rates, however, of the same whistle type as the stimuli sharply increased in the minute after the playback in comparison to the preceding minute (Figure 6.3). It may be that other responses are given as a result of being

'addressed', such as the movement towards the caller's location. One caveat of this study is that the location of the target animal (signature whistle owner) was unknown. Movement response was taken from the closest animal before and after the playback. If the target animal was not the closest animal it would not have been possible to detect whether the animal approached the speaker upon hearing the playback. In the instance of treatment 7 it may be the animal approached the caller's location before it started calling back in response. To overcome this problem, the signature whistles of individual animals would need to be known. The recent development of a method to identify signature whistles in free-ranging animals, as used in this study, goes some way to address this problem (Janik et al., 2012). It is, however, difficult to associate each signature whistle with an identifiable animal with acoustic localization in real time. A more favorable approach would be to conduct the same experiments on wild bottlenose dolphins in Sarasota Bay, Florida (Wells, 2003; Wells et al., 2004). The population is well-studied with the signature whistles of more than 150 animals recorded in temporary-capture events (Sayigh et al., 2007). This would allow a focal animal to be chosen and its movement and behavior closely monitored throughout the playback experiment.

One other problem with the study may lie in the accuracy of the stimulus used. The whistles used in the playbacks are exact synthetic replicates of the signature whistles recorded from the group. We know dolphins produce signature whistle copies with parameter differences, in comparison to the original whistle, that may act as acoustic cues to the identity of the caller (Chapter 5). The lack of these parameter differences means that there may be an unnatural element of the stimulus in our playbacks that may account for only 6 of the playbacks eliciting a response.

However, not all copies are distinguishable from the original signature whistle, with some being highly accurate representations (chapter 5), therefore the use of exact synthetic replicates should not be a problem. The synthesised whistles also go some way to addressing this problem as all the voice features of the animal are removed (Janik et al. 2006), and we know dolphins respond to synthesised whistles in a biologically meaningful way (Janik et al. 2006). Finally, although every effort was made to ensure that all group members were present during the playback it may be that our target animal was either no longer with the group, was too far from the boat at the time of playback resulting in the signal being too faint to elicit a reaction, or lacked sufficient motivation to respond vocally.

Vocal production learning has led to the development of individually distinctive calls in bottlenose dolphins, while at the same time making them capable of copying the whistles of other individuals. Evidence of actual referential communication, however, is still sparse. For a signal to function as an external referent it must meet two requirements. It must be structurally discrete with a high degree of stimulus specificity (Macedonia & Evans 1993; Wanker et al., 2005; Evans 1997). Signature whistles fit neatly in here; their arbitrary nature and the high inter-individual variability make them specific to each individual animal. Secondly, the response of the receiver should be elicited by the signal even in the absence of contextual information (Macedonia & Evans 1993; Evans 1997). Spectacled parrotlets respond strongly to calls directed at them, even when the interacting bird is not present (Wanker et al., 2005). I have shown here that bottlenose dolphins also respond to calls directed at them, even when the caller is not known, and although further work is needed to ensure the identity of the calling animals, these results provide compelling evidence that bottlenose dolphin signature whistles may be function referentially.

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Chapter 7

General Discussion

7.1 Introduction

The bottlenose dolphin (*Tursiops truncatus*) is a highly social species that forms complex fission-fusion societies (Connor et al., 2000). It remains one of the best studied cetacea, both in captivity and in the wild, allowing a number of cognitive questions to be addressed.

The bottlenose dolphin is not the only animal to form complex societies, both primates and birds contain species with similar social structures. All three taxa show evidence for vocal learning, allowing interesting comparisons between species that may shed light on the evolution of human language (Janik 2009; Catchpole & Slater 2008; Egnor & Hauser 2004). Over the years bird song has been a highly influential model system to address evolutionary questions on vocal learning and complex vocal communication (Catchpole & Slater 2008). Although vocal learning is common in birds, it is less so in mammals, with only a few species found to be capable of vocal learning: bats (Boughman 1998; Knornschild et al., 2010) elephants (Poole et al., 2005), pinnipeds (Ralls et al. 1985; Janik & Slater 1997) , primates (Egnor & Hauser 2004; Mitani & Gros-Louis 1998) and cetaceans (Tyack & Sayigh 1997; Janik 2009). These mammalian species can also provide insight into the selection pressures governing vocal learning.

Delphinids, for example, are particularly interesting largely due to the mechanisms they use for individual recognition in an underwater environment. Surprisingly, many similarities can be drawn between delphinids and humans, namely they both have large brains

(Marino 2004), they both live in complex societies (Connor et al., 2000), and both communicate with an extensive repertoire of learned signals (Caldwell et al., 1990). As in human language, social learning is important in delphinid communication, with vocal production learning playing a paramount role in the imitation of individually specific calls (Tyack & Sayigh 1997), in the production of vocal labels (Richards et al. 1984), and in the formation of regional dialects (Ford 1991) .

The bottlenose dolphin is a delphinid species that uses vocal learning to develop its own individually specific signature whistle early in life (Tyack & Sayigh 1997; Miksis et al., 2002; Fripp et al., 2005). Dolphins will copy one another's individual signal, indicating that signature whistles may be used to label or address social companions. Yet, so far, the cognitive significance of the use and imitation of signature whistles remains uncertain. In this thesis, I utilised a number of tools and techniques to explore the imitation of signature whistles, both in captive animals and temporarily-restrained and free-swimming wild animals. It is hoped that the outcomes of this thesis can contribute to the broader understanding of how different species use vocal learning and vocal imitation to develop and maintain individually specific bonds, and to understand the selection pressures that govern the development of different communication strategies.

7.1.2 Why do dolphins whistle match?

Vocal matching has been discussed in depth throughout this thesis. The studies on song type matching in songbirds have always been clear in their definitions. The diffusion of vocal matching studies into the wider literature has led to some confusion as to what constitutes vocal matching. Chapter 2 proposed a strict set of criteria that could be applied to vocal exchanges to determine if they are true vocal matching events.

A broad definition, where a vocal interaction must meet the following criteria: (a) animal B produces the same signal as animal A, (b) animal B produces the signal immediately after animal A and (c) this should occur at a higher proportion than chance levels, would allow studies on different taxa to become more comparable.

Tools can be implemented that may assist in identifying a vocal match using this criteria. These tools, as described in chapter 2, have been implemented throughout this thesis. Playback studies formed a central component to chapter 3, which addressed how animals responded to being vocally matched. The study allowed observations of the fine-scale responses of individuals to matching interactions. The playback experiments identified the time window (< 1 second) from whistle to playback after which a vocal response is likely to be produced by the subject. Vocal matching therefore should occur immediately after the signaller calls in order to elicit a response. This temporal exchange is also seen for the counter-calling of different call types in the bottlenose dolphin (Nakahara & Miyazaki 2011). It may be that if animals call at time intervals of > 1 second after the initial signal the response may not be directed at the signaller. These experiments have shown that there is an increased probability of animals responding to a match by calling back.

This use of interactive playback with marine mammals is a novel approach that can give a greater insight into the function of certain vocal behaviours. These experiments have revealed that vocal matching in dolphins is an effective signal for addressing individuals with no associated signals of aggression or avoidance behaviour given to the matching playbacks. We know that the copying of signature whistles primarily occurs between close social affiliates (Chapter 5). Signature whistle matching in dolphins therefore appears to be a way for close social companions to address one another. This makes for an interesting comparison between taxa. Songbirds use song type matching to escalate aggressive interactions. Bottlenose dolphins use vocal matching to maintain contact with closely bonded animals. Yet the striking

similarity is that for both taxa vocal matching is used to address another individual. Vocal matching therefore may have developed across taxa under different selection pressures but for ultimately the same purpose.

Randomisation tests have been used in previous studies to test for vocal matching (Janik, 2000; Miller et al., 2004; Schulz et al., 2008). Chapters 4 and 5 used randomisation techniques to confirm the occurrence of whistle matching, showing it did indeed occur at above chance levels. Chapter 4 investigated the occurrence of rapid whistle matching in wild animals. The study was somewhat restricted because whistles could not be localised to individuals. Vocal matching could therefore have been produced at higher rates than detected. Instead the overlapping of the same whistle type was used to identify matching events. The study revealed that rapid vocal matching plays a specific role in bottlenose dolphin foraging behaviour. The occurrence of overlap matching was significantly above chance levels, which differs from overlap matching in songbirds (Searcy & Beecher 2009). In songbird species the overlap of the same call type has been discussed as a signal that escalates an aggressive interaction (Naguib & Mennill 2010). Other authors contest this on the basis that overlap matching does not occur above chance levels and as such may not even be a signal at all (Searcy & Beecher 2009; Searcy & Beecher 2010). The function of this vocal behaviour in bottlenose dolphins remains unknown, although the results of the playback experiments indicate that it is unlikely to be aggressive. Many animals are known to coordinate group movement (Wilkinson & Boughman 1998; Radford & Ridley 2008), or to maintain within-group contact during foraging (Jones & Ransome, 1993; Miller et al., 2004; Mitani & Nishida, 1993; Schulz et al., 2008; Sugiura, 1998).

Animals producing the same call type simultaneously may be doing so affiliatively as a form of vocal accommodation (Tyack 2008). The temporary convergence of calls in chorusing bouts occurs in chimpanzees (*Pan troglodytes*) (Mitani & Gros-Louis 1998). The

overlapping of same whistle types, however, primarily occurred during foraging. If the overlap matching of whistle types plays a role in strengthening social bonds we may expect it to occur in a social setting rather than during foraging behaviours. Anecdotally, in this study the bottlenose dolphins appeared to largely produce only 3 different whistle types in these overlapping interactions. It may be that same whistle type overlap may therefore function as excitement calls, a result of social or feeding excitement. Delphinids are known to produce specific call types during high arousal behaviours (Rehn et al., 2011).

Future work should implement a localisation system to try and identify movements of the animals before and after a matching event. A study would need to identify whether overlap matching facilitates joins between animals, or perhaps occurs before animals move locations. A cross-population study would be interesting, to see whether this behaviour is unique to this East Scottish population, or whether overlap matching is a universal signal in bottlenose dolphin foraging behaviour.

7.1.3 The role of vocal imitation

Long-term studies can provide invaluable information on the life history of a species and on their vocal repertoires. The population of bottlenose dolphins in Sarasota Bay, Florida, USA, have been extensively studied. Vocalisations of individual wild dolphins can be recorded during annual captures of wild dolphins, which are conducted for health assessment purposes (Wells 2003). Thus the signature whistles of over 200 wild animals have been identified (Sayigh et al., 2007). The imitation of individually specific calls is very difficult to show in wild animals. The unique data set used in chapter 5 allowed the occurrence of vocal imitation of signature whistles in wild, temporarily-retrained animals to be investigated. Spectrographic analyses were then conducted to look at differences between the vocal copies and the original calls.

The previous documentation of signature whistle imitation led to the question of how dolphins would recognise an animal producing another dolphin's signature whistle contour. One possibility would be the context in which the whistle is copied. If it is only produced in an exchange between two animals then identity is easy to track (Harley 2008). In chapter 5 I showed that the imitation of another dolphin's signature whistle occurred almost exclusively between close associates. The copies were clearly recognisable as such since copiers consistently modified selected acoustic parameters of a signal when copying it. Bottlenose dolphins can detect subtle frequency parameter differences (Harley 2008; Thompson & Herman 1975), so these differences between copies and originals are likely detectable to the dolphins. This may be important because if signature whistle copies were not discernible from the original signature whistle then the signature whistle identity system may become unreliable. I have shown that instead animals may distinguish between original signature whistles and their copies by the presence of acoustic cues. It is important to note that not every copy appeared to be distinguishable from the original signature whistle, and highly accurate renditions do occur. This is important in the context of the signature whistle playbacks where synthesised original signature whistles were used. The use of the animals' own signature whistle may have had some influence on the high response rate, similar to self-song playback in birds (Falls et al.,1982). However, 'self-song' playback in songbirds has only occurred with unprocessed song recorded directly from the bird. They are therefore difficult to interpret functionally. The synthesised whistles used in dolphin playback studies go some way to addressing this issue by removing all voice features from the whistle, with dolphins still responding to them in a biologically meaningful way (Janik et al,, 2006).

It is important to try and distinguish between vocal copying, where one animal copies another animal's individually distinctive call, and vocal convergence where animals converge onto one shared call type. Previous studies have demonstrated the vocal convergence of allied male dolphins onto a shared signature type (Smolker & Pepper, 1999; Watwood et al., 2004).

This study documented signature whistle copying between two pairs of allied males, one of which had formed a long-lasting association. Data for this pair spanned 12 years, across which the pair continued to produce their own non-identical signature whistles as well as copying the finer details of each other's preferred whistle type. Signature whistle copying was also observed between mother and calves who were equally likely to copy one another. There is some evidence female calves produce signature whistles that are distinct from their mothers (Sayigh et al., 1995). Furthermore, the signature whistles of adult bottlenose dolphins have been shown to be stable for periods of over a decade (Sayigh et al., 1990; Sayigh et al., 1995). This study shows that mothers and calves with distinctly different signature whistle types will vocally copy one another. The fact that females, as well as males, will copy one another's signature whistle offers support to the interpretation that signature whistle copying is not an early stage in the process of vocal convergence.

The study also revealed that animals who engaged in copying had strong social relationships. The balance of the evidence therefore leans towards the interpretation that the function of signature whistle copying is for social affiliation. It is unlikely that copying is aligned with aggression as it was not common between animals of low association levels. This is also supported by the results from chapter 3, where the copying of signature whistles in vocal matching interactions elicited no signs of aggression or avoidance behaviour in the animals. The results contrast with species that have large shared repertoires, such as songbirds, where the use of copying in vocal matching interactions appears to be functionally agonistic.

Chapter 6 addressed the *signature labelling hypothesis*, an idea that an individual can initiate an interaction with a conspecific by imitating its signature whistle (Tyack 1993). This idea of signature whistles being used as descriptive labels, similar to human names, is intriguing. The naming of individuals with vocal labels has so far not been reported in the

animal kingdom. Yet studies with captive animals show it may be present in parrots (Pepperberg 1981; Wanker et al. 2005) and dolphins (Richards et al. 1984). Both of these taxa form complex social structures and are capable of vocal imitation. Since captive dolphins can be trained to use learned acoustic signals to label objects (Richards et al., 1984), then perhaps their learned identity signal can be used as a name-like tag or label.

The study showed, through playback experiments, that dolphins do respond to hearing a copy of their signature whistle by calling back. Animals responded to calls directed at them, even when the identity of the caller was unknown to the animal. The study, which was conducted in St Andrews Bay, did have some limitations, particularly because the target animal could not be identified. The field site of Sarasota Bay, where the signature whistles of individual wild animals are known, would be an excellent alternative site. Here the identity of the target animal would be known prior to playback, and its individual response could be closely monitored. The project would benefit from the incorporation of DTAGs (Johnson & Tyack 2003), which may be used to monitor an animal's response to playback. DTAGs record sound, depth and orientation of an animal using suction cup attachment. This would allow both the vocal and behavioural response (including movement) of the animal to be analysed. The study presented in this thesis has, however, provided compelling evidence that bottlenose dolphin signature whistles may be used as referential signals. Thus supporting Tyack's (1991) *signature labelling hypothesis* and the idea that signature whistles are used as vocal labels to address or refer to individuals, similar to human names.

7.4 Conclusions

This thesis provides the first intensive study on the vocal imitation of individually specific calls. The copying of signature whistles appears to be relatively rare, which may help preserve the honesty in the signature whistle identity system. Dolphins are likely to detect the acoustic differences that are found between original signature whistles and their copies (Chapter 5). These differences, however, may not be discernible at distance due to the effects of sound degradation. Frequent use of signature whistle copies may therefore make the signature whistle an unreliable indicator of identity within the large communication network of the bottlenose dolphin. I have established that the vocal imitation of signature whistles is primarily an affiliative signal with no evidence for its use in aggression or deception. Vocal matching in dolphins, as in songbirds, functions as a way of addressing individuals. This may help at times when coordination and cohesion are important such as during cooperative foraging. In the song sparrow (*Melospiza melodia*) it is also a signal of aggressive intent (Searcy & Beecher 2009). In the bottlenose dolphin, however, its use is markedly different with no evidence of an aggressive function. Finally, it appears signature whistle copies can be used as vocal labels to address specific individuals.

Future work should explore the use of identity signals in other social species that show vocal learning, such as elephants and parrots. It would be interesting to compare their use of contact calls, the encoding of individual identity, and the role of vocal learning in vocal imitation and referential communication. Such a comparative approach would help shed light on whether vocal learning developed in these different social species under similar selection pressures as a way of maintaining individually specific bonds, and to understand the evolutionary implications of their communication strategies.

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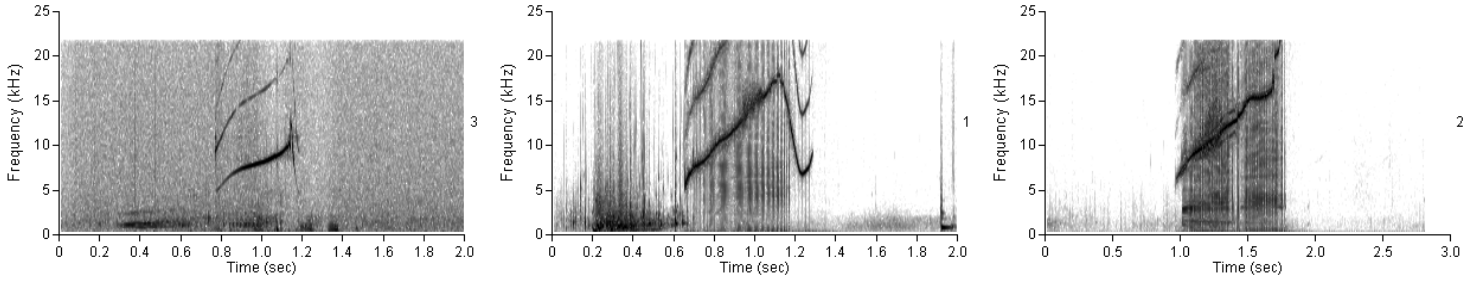
Appendices

Appendix 1

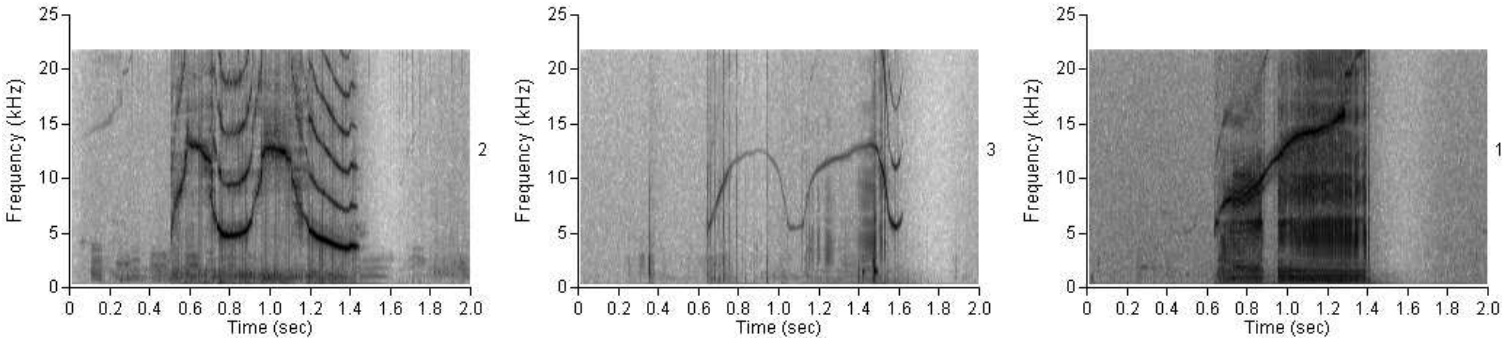
Examples of signature whistle copies; the signature whistle of the owner (left); the copy (middle), and the copier's signature whistle (right).

a.



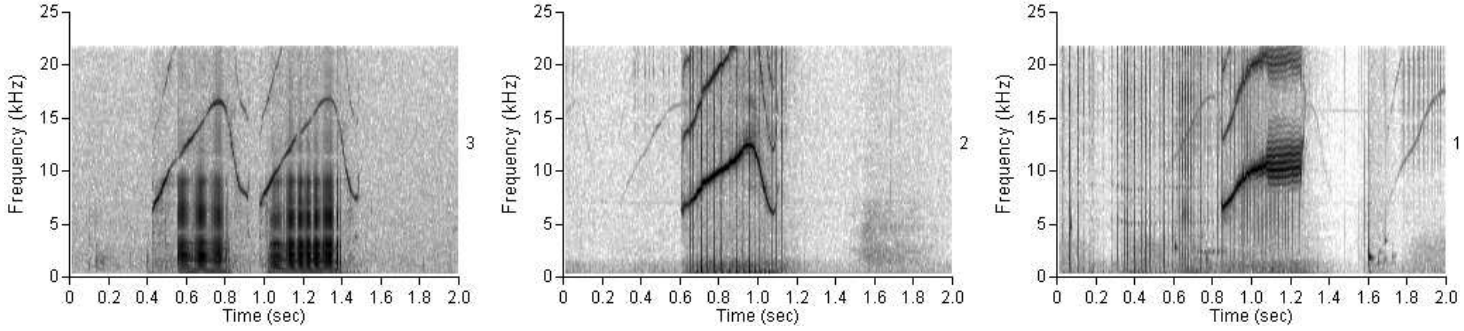
Calf FB 55 (left) is copied (middle) by mother FB 5 (right).

b.



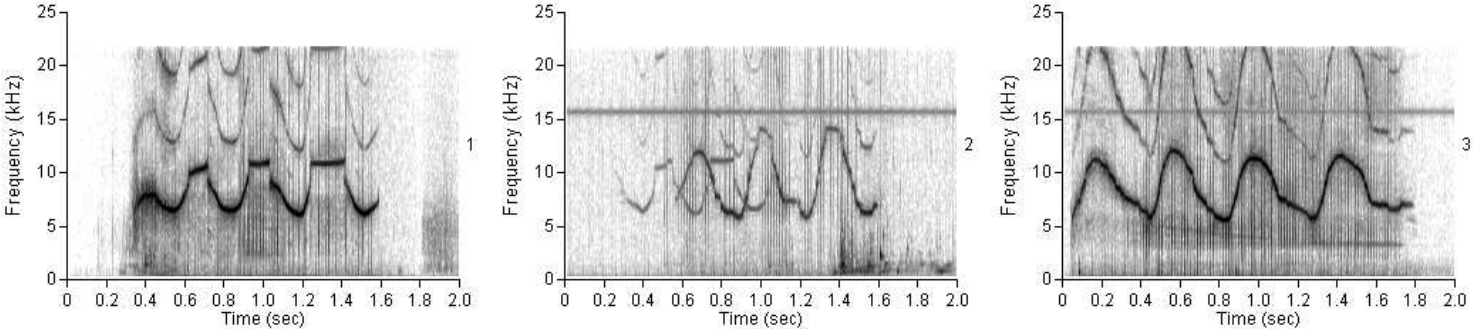
Calf FB 155 (left) is copied (middle) by mother FB 5 (right).

c.



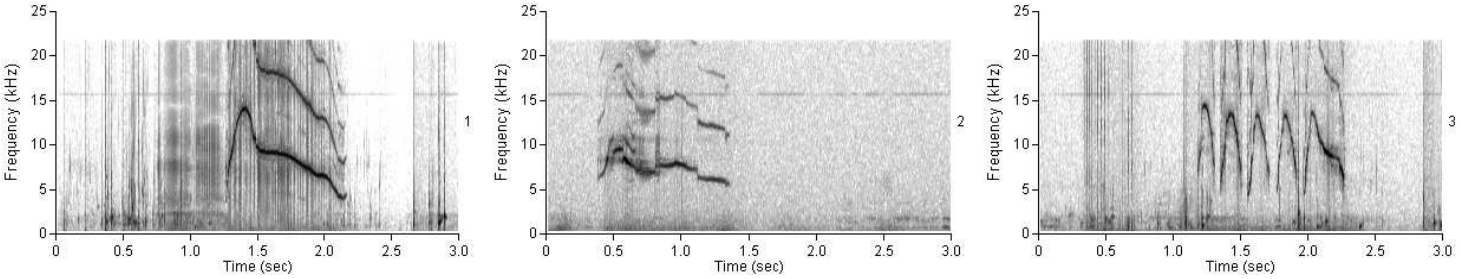
Calf FB 177 (left) is copied (middle) by mother FB 9 (right).

d.



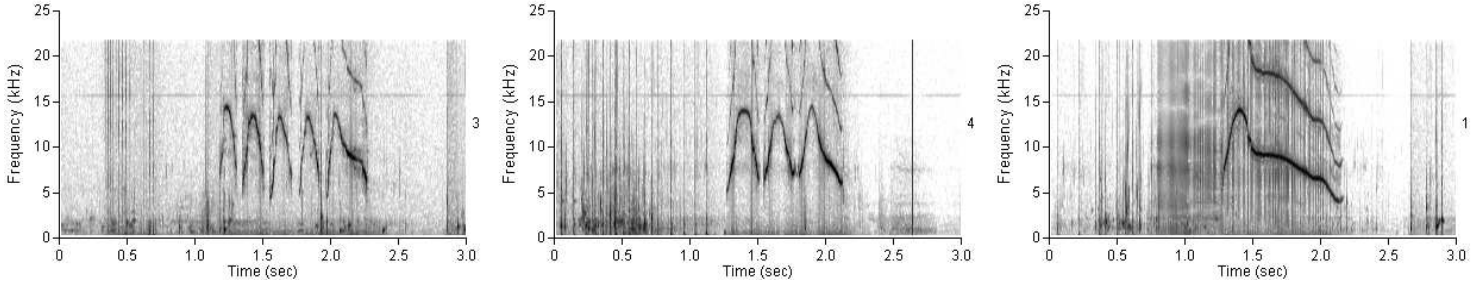
Male FB 20 (left) is copied (middle) by male FB 114 (right).

e.



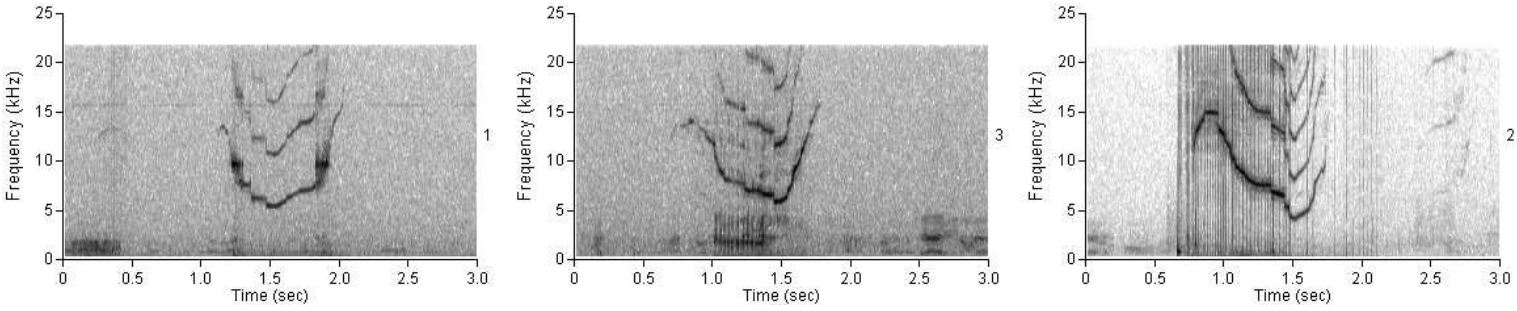
Male FB 26 (left) is copied (middle) by male FB 48 (right).

f.



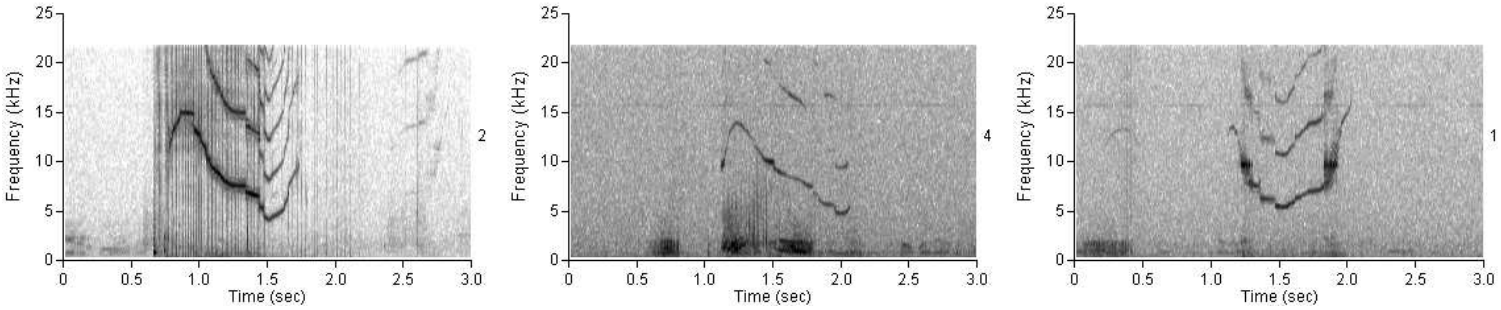
Male FB 48 (left) is copied (middle) by male FB 26 (right).

g.



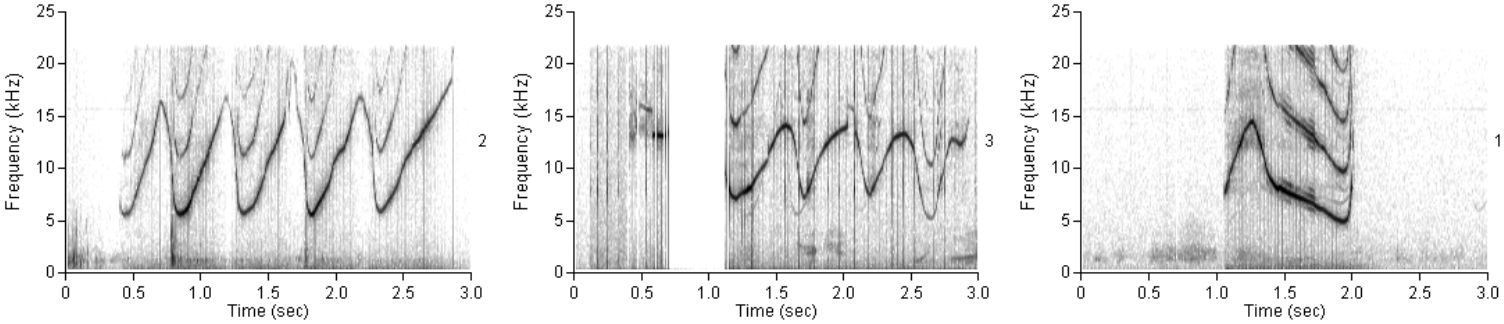
Mother FB 35 (left) is copied (middle) by calf FB 93 (right).

h.



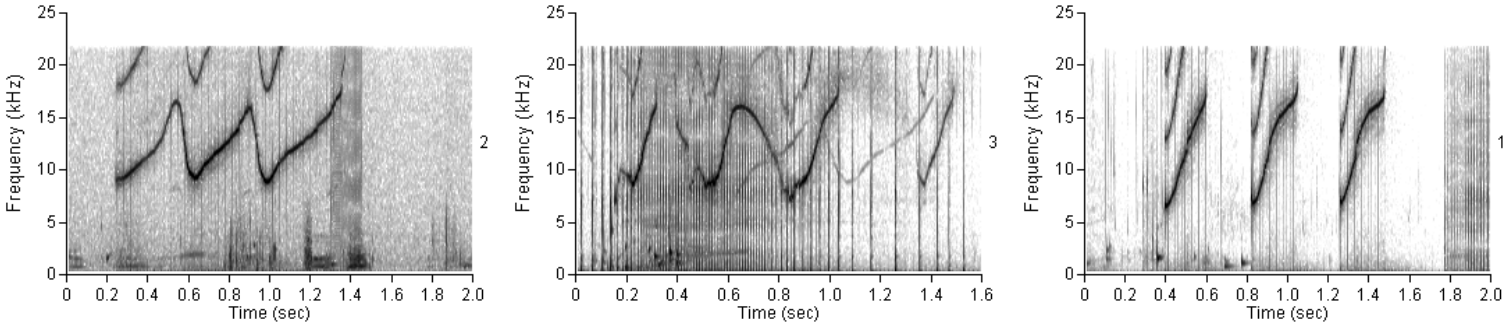
Calf FB 93 (left) is copied (middle) by mother FB 35 (right).

i.



Mother FB 67 (left) is copied (middle) by calf FB 65 (right).

j.



Calf FB 95 (left) is copied (middle) by mother FB 71 (right).